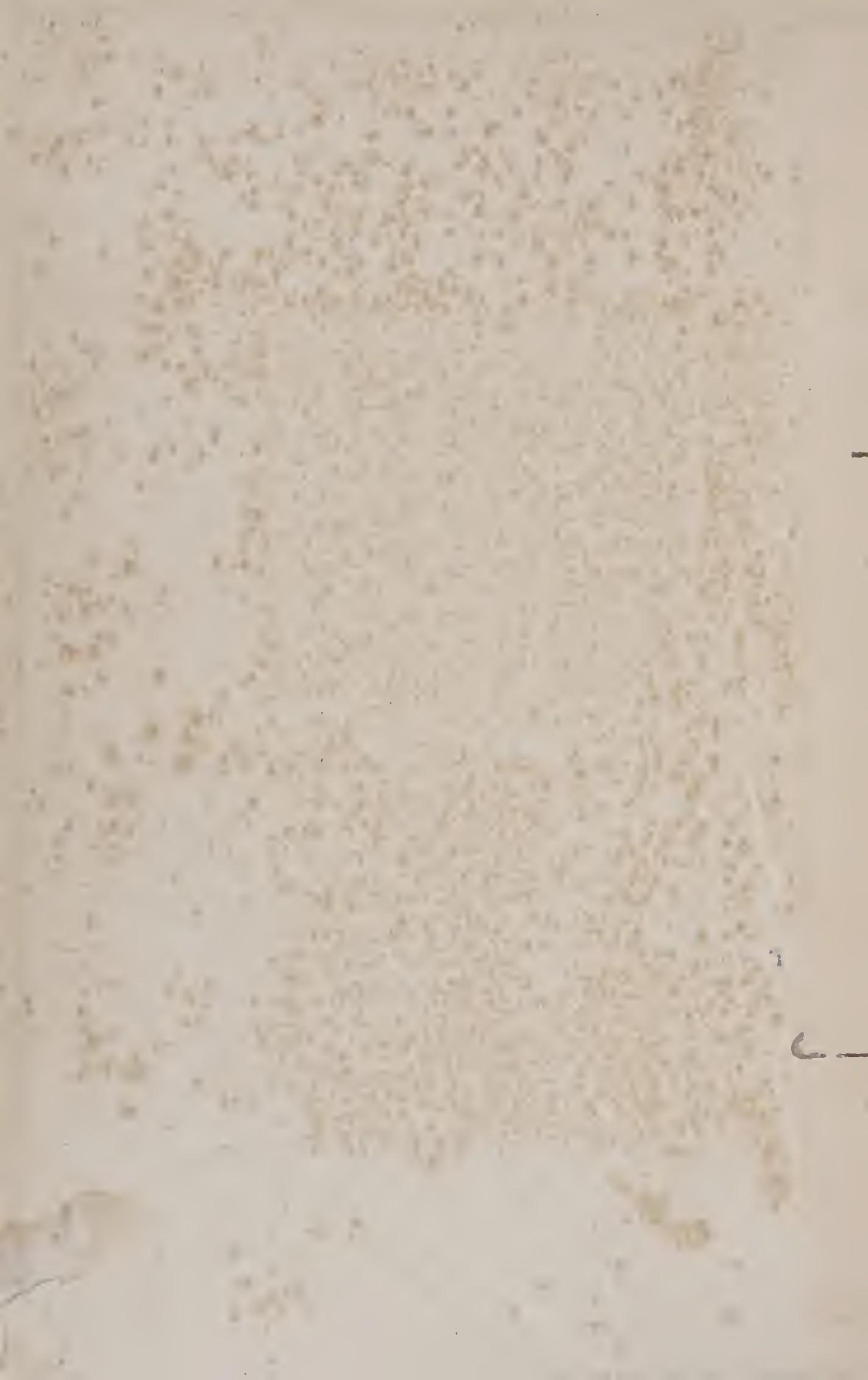


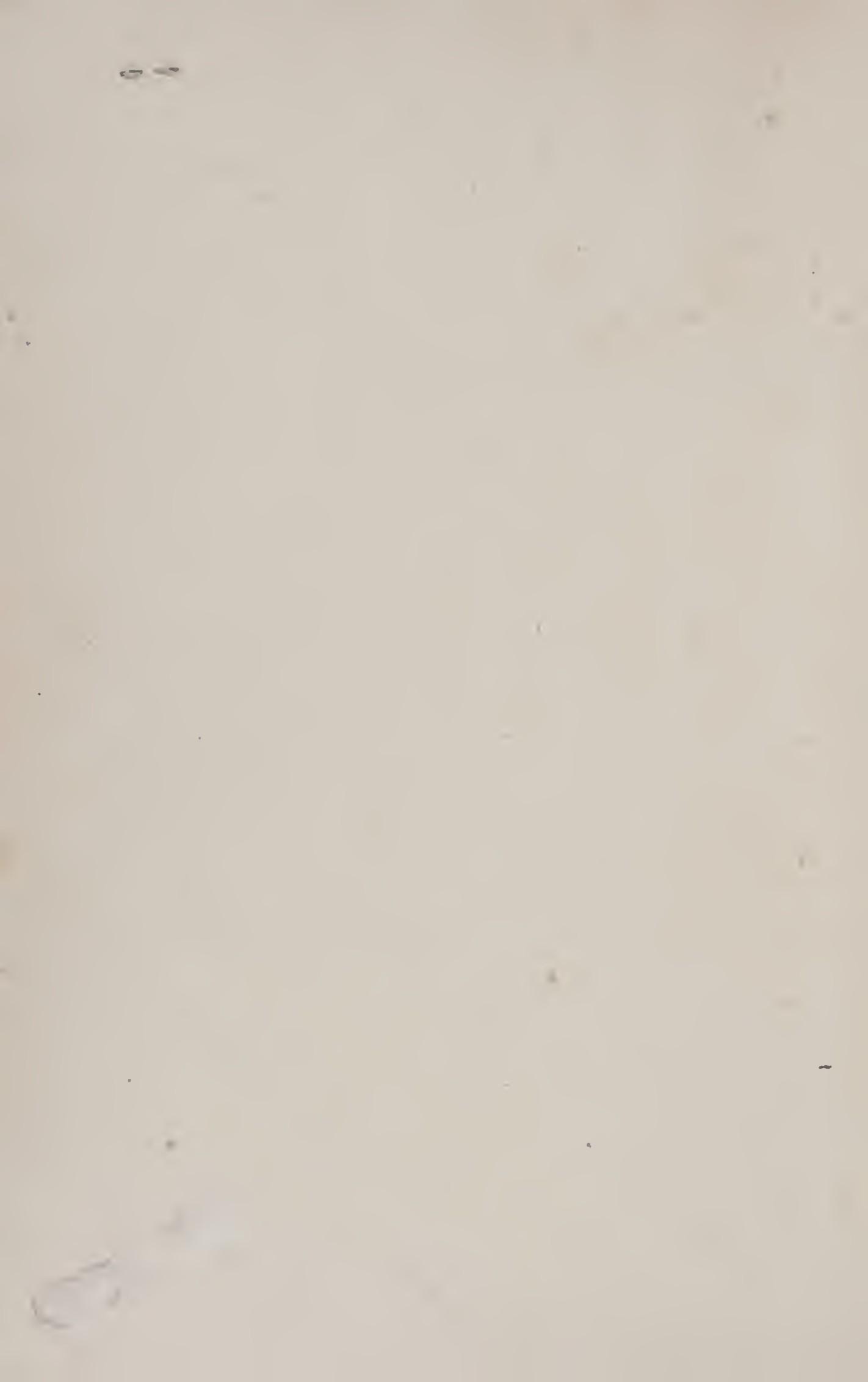
HERMAN E. HAWKARD

THE STRUCTURE OF
ECONOMIC PLANTS



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THE STRUCTURE OF ECONOMIC PLANTS



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THE STRUCTURE OF ECONOMIC PLANTS

By

HERMAN E. HAYWARD

*Professor of Botany
The University of Chicago*



New York

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1948

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*To
My Mother and Father*

PREFACE

THIS book is an outgrowth of courses in plant anatomy offered at the University of Chicago since 1927. Much valuable anatomical work has been done in the form of monographs on specific plants, special studies of restricted scope, general studies of organography, and in studies incidental to research in physiology, pathology, pharmacology, and other fields of plant science. Discussions with those interested in applied botany, research workers and students, suggested the desirability of preparing a work which would bring together some of these investigations relating to the structure and developmental anatomy of a number of economic plants. In this book, the available data have been freely drawn upon, and at the conclusion of each chapter there is appended a selected list of citations from which material has been obtained. There has been no attempt to compile a complete bibliography, but the selections have been made that more detailed information on special phases of plant anatomy may be readily available. In many instances, the citations listed have extensive bibliographies.

The book has been organized in two parts, the first dealing with general plant anatomy, the second with the structure of a selected number of economic plants. In Part I, the point of view of developmental anatomy has been presented briefly, together with the nomenclature which is used in Part II. Since nomenclature is frequently inconsistent, a glossary defining the terms in the sense in which they are used in this work is appended. The introductory chapters are intended to supplement other works on anatomy and to make this work more generally useful.

In Part II, it was obviously impossible to consider a large number of plants in as great detail as the amount of material available and the usefulness of such material to investigators would warrant. The problem of which to include and which to omit presented a real difficulty. The principal criteria determining the selection were the economic importance of the plant, its suitability as a representative of the family to which it belongs, and the intricacy

of its anatomical and morphological detail. Important fruit crops have been omitted because a second volume is contemplated which will deal more especially with them.

ACKNOWLEDGMENTS

The preparation of this work has been greatly aided through the generous assistance of fellow workers in the fields of botany and agriculture. Many have contributed the results of their researches and illustrative material, and the author expresses his deep appreciation of this cooperative spirit which has made possible the inclusion of valuable data. Individual acknowledgment accompanies the text and illustrations in each case. Thanks are due The University of Chicago Press for permission to use illustrations from the *Botanical Gazette*. Acknowledgment to other journals, publications, and publishing houses appears at the point of insertion of the material used.

The preparation of the original plates was aided in part by a grant to the University of Chicago from the Rockefeller Foundation. The original line drawings and photomicrographs were prepared by the author and associated students, especially Miss Jean Port, who also aided in the preparation of the manuscript. The author is deeply indebted to Professor E. J. Kraus, who read the entire manuscript, for valuable suggestions and encouragement from the inception of the idea of the book to its final completion.

HERMAN E. HAYWARD

CHICAGO, ILLINOIS

September, 1938

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THE STRUCTURE OF ECONOMIC PLANTS



PART I. GENERAL ANATOMY

CHAPTER I

CELLS AND TISSUES AND THEIR DEVELOPMENT

IN the description of the structure and development of the seed plant, it is convenient to consider separately its major vegetative organs, *root* and *shoot* (*stem* and *leaves*); and, more or less intimately, its structures associated with gametic reproduction, the *flower* and *fruit*. The *organs* may be resolved into their constituent *tissues*; and these, in turn, into types and groups of *cells*, constituting a simple tissue, that are essentially alike in structure and in the functions they perform.

THE CELL

The term *cell* has been variously applied. Early microscopists interpreted it as the box-like unit of structure of which plant and animal tissues are comprised, obviously referring to the cell wall rather than to any included matter. Later, emphasis shifted to the cell contents, or *protoplasm*, rather than the wall. On this basis, a *cell* may be defined as a *protoplasm* which usually consists of a *nucleus*, *cytoplasm*, and various *inclusions*. (Fig. 1.) The term *cell* is still applied, however, in cases in which the protoplasm is lost in the process of differentiation and maturation. Thus tracheids, vessel segments, and various types of sclerotic elements which have no protoplasm at maturity are frequently referred to as cells in descriptive anatomy although it is preferable to use the term *element* in such cases. The most significant investigations relative to the detailed structure of the cell have been treated by Wilson (45) and Sharp (40). For this reason, the following account is restricted to those aspects of cytology which are most frequently associated with the problems of developmental anatomy.

THE PROTOPLAST. — The *protoplasm* is commonly differentiated into several parts: *cytoplasm*, *nucleus*, *plastids*, and other cell *inclusions*.

The cytoplasm constitutes the main mass of the protoplast, and at its limiting outer periphery is the *plasma membrane*. Physically, cytoplasm is a colloidal system, probably of the emulsion type, with properties similar to those of other recognized colloids such as viscosity, adsorptive power, semi-permeability, and its structural

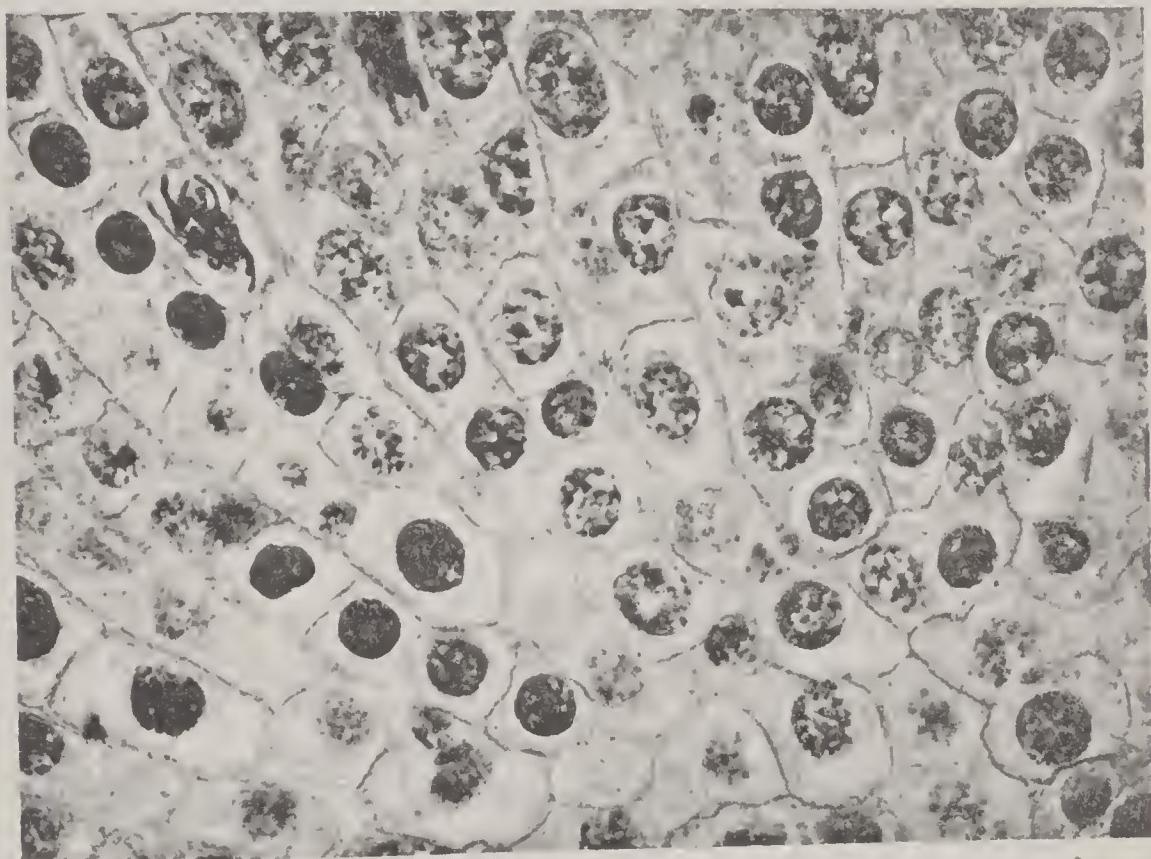


FIG. 1. Meristematic cells from the growing point of the root of *Lilium Harrisii* showing character of the cytoplasm and nuclear activity.

reactions to external and internal factors both chemical and physical. Optically, cytoplasm appears to be a hyaline, homogeneous semi-fluid with numerous inclusions (granules, globules of fat and oil, chondriosomes, plastids, etc.) which occur in varying sizes and frequencies. The physical appearance of the colloidal system may be modified by the degree of viscosity of the cytoplasm as well as by the extent and character of vacuolization. In a young meristematic cell, the cytoplasm is relatively dense with numerous minute vacuoles; but, as it matures, these become fewer and larger until finally a large central vacuole or sap cavity is formed. In this case, the protoplast is limited centripetally by a *vacuolar membrane* and

is restricted to a narrow peripheral layer within the cell wall. In cells where the nucleus is centrally located, strands of cytoplasm may extend to it from the periphery.

As Sharp has pointed out: "It cannot be maintained that anything like an adequate chemical picture of living protoplasm has been obtained." The protein content is high, consisting of peptones, albumins, and globulins; but relatively little phosphorus is present, except in the nucleoproteins of the nucleus. The fatty substances most commonly found include true fats and other fatty compounds such as cholesterol and lecithin. Carbohydrates occur most frequently as pentoses, and inorganic salts have been recognized in increasing numbers. The amount of water present is large, varying with the type of tissue and its degree of maturity.

THE NUCLEUS.—The nucleus is conspicuous in meristematic cells; but, as demonstrated by Bailey (3) in cambial initials, there is no constant relationship between the volume of the nucleus and that of the cell as suggested by Strasburger and others. It usually occupies a more or less central position in the cytoplasm, but this may depend upon the degree of vacuolization of the cell, since it always lies embedded in the cytoplasm. It is commonly spherical or ellipsoidal and is bounded by a thin nuclear membrane within which is a transparent substance known as the *karyolymph* or *nuclear sap*. In this sap is a *reticulum* of threads which are associated with or constituent parts of the filamentous portions of the chromosomes. The existence of the reticulum as a valid nuclear structure has been questioned; but, on the basis of critical comparisons between living nuclei and those to which various fixatives have been applied, it seems to be established that it is in no sense an artifact. The reticulum has been regarded as a dual structure consisting of a framework of *linin* supporting granules of *chromatin*, but the more recent and probably more generally accepted view is that it consists of a single complex substance, *karyotin*. One to several *nucleoles* may occur in the resting nucleus which appear as viscous droplets and are composed of proteins and lipins.

No complete statement regarding the function of the nucleus can be made, but it is associated with the process of cell division and directly or indirectly with wall formation. It undoubtedly plays an important role in the later development and differentiation of the cell, and is intimately concerned in the cellular metabolism. From the genetic standpoint, it may be regarded as carrying and

transmitting the heritable characters of the organism; but some instances of cytoplasmic or plastid inheritance have been demonstrated.

PLASTIDS. — Plastids are the most conspicuous structures in the protoplast and occur in some of the tissues of practically all plants with the exception of certain groups of Thallophytes (Cyanophyceae, and fungi). Like the nucleus, they lie in the cytoplasm and are not known to occupy vacuolar cavities. They are variable in shape, being spherical, ovoid, or discoid; but the size is relatively constant. Möbius (29) found that 75 per cent of the plastids in 215 species of plants examined had a long axis ranging from 4 to 6 μ . Among those which fall within the average range are the plastids of *Cucurbita*, *Gossypium*, *Lactuca*, and *Phaseolus*; in *Beta* they are larger, ranging from 7 to 10 μ .

The manner in which the plastids originate is not entirely clear; but, in most instances, it appears that they arise by the division of preexisting plastids or from proplastids. Randolph (35), working with *Zea*, was able to observe the behavior and development of proplastids in living cells and noted the formation of mature plastids from minute granular proplastids. Early stages occur in the tips of leaf primordia, transitional ones appear near the apices of successively older seedling leaves not yet exposed to sunlight, and later stages may be found in leaves that are about to emerge from the surrounding sheath. In cells of the mesophyll of well-developed seedling leaves, the chloroplasts have a diameter of 7 to 8 μ .

Whether or not the proplastids are always formed from other cytoplasmic inclusions such as chondriosomes, or arise *de novo*, is not established. Randolph has concluded that "the question regarding the extent to which the plastids are to be considered permanent cell organs with an unbroken genetic continuity throughout the life cycle must remain an open one"; and Sharp (40) has reasoned that "if plastids represent transformations of the cytoplasm resulting from the localization of certain processes, they may well be expected to differentiate anew as these processes begin, and to preserve varying degrees of permanence depending upon the processes carried on." On the other hand, Bowen (9), working with the root tissues of several plants including *Pisum*, *Hordeum*, *Cucurbita*, and *Phaseolus*, concludes that "it is perfectly clear now that plastids are formed only by the division of preexisting plastids."

The principal types of plastids are *chloroplasts* found in photosynthetic tissues (chlorenchyma), and colorless *leucoplasts* which occur in meristematic tissues and in the cells of storage organs. The latter are sometimes more specialized, and are known as *amyloplasts* because of their relation to the formation of starch reserves. *Chromoplasts*, other than chloroplasts, may contain many of the color pigments found in flowers and fruits. The carotene in the fruit of the tomato occurs inside the plastids; and, after their decomposition, in free crystalline or globular form. The yellow and a few of the red pigments of many flowers and vegetative structures may be localized in plastids; while others are in solution in the cell sap, such as the anthocyanins in the fleshy root and hypocotyl of beet or radish.

Various cell inclusions may be sufficiently characteristic to be helpful in anatomical diagnosis. These include crystals of calcium oxalate, calcium carbonate, silica, inulin and protein crystals, aleurone grains, starch, and semi-solid compounds classed as gum, resin, fat, mucilage, or latex. The cell sap may contain salts, carbohydrates, proteins, alkaloids, and pigments in solution which can be used in micro-chemical diagnosis, and similar techniques are applied in cell wall analysis.

THE CELL WALL. — With few exceptions, the cells of seed plants have walls that are formed by the activity of the protoplast. The character of the cell wall is important in tissue analysis since various cell types have been named on the basis of differences in its structure. The mature wall is generally regarded as a non-living membrane; but it is commonly penetrated by cytoplasmic strands, *plasmodesma*, which may be either primary or secondary in origin. The primary type is present during the formation of the primary wall and persists thereafter, while the secondary type develops later by penetration. The plasmodesma may be aggregated into groups to form conspicuous strands, or sometimes occur as evenly distributed single threads — in which case they are difficult to demonstrate because of their extreme fineness. The penetration of the wall by these cytoplasmic threads is thought to establish protoplasmic continuity in living tissues, and it is probably not inaccurate to regard the young wall as consisting in part of living matter. In any event, the interrelation between the development of the wall and the protoplast is very intimate, since the growth of the former is conditioned upon the activity of the latter.

The terminology used with reference to the constituent parts of the cell wall has been confusing and contradictory, but Kerr and Bailey (25) have proposed a system of nomenclature with which Frey-Wyssling (19), Anderson (1), and others working on cell structure are in general agreement. Briefly summarized, they suggest that the term *primary wall* "should no longer be applied to the first formed layer of secondary thickening, but should be used

solely in designating the cambial wall and its homologues in other tissues." With reference to the term *middle lamella*, they suggest that "it should be used synonymously with *intercellular substance* in referring to the truly isotropic layer of intercellular material." These recommendations are based upon investigations which indicate that cambial initials have walls that are independent morphological structures composed chiefly of cellulose and pectic substances and that they are anisotropic; while the intercellular substance (middle lamella) between the walls of adjacent initials is an amorphous, isotropic colloid, composed largely of pectic substances deposited by the cytoplasm. (Fig. 2, A, B.) An important characteristic of the intercellular substance is its plasticity, which permits the

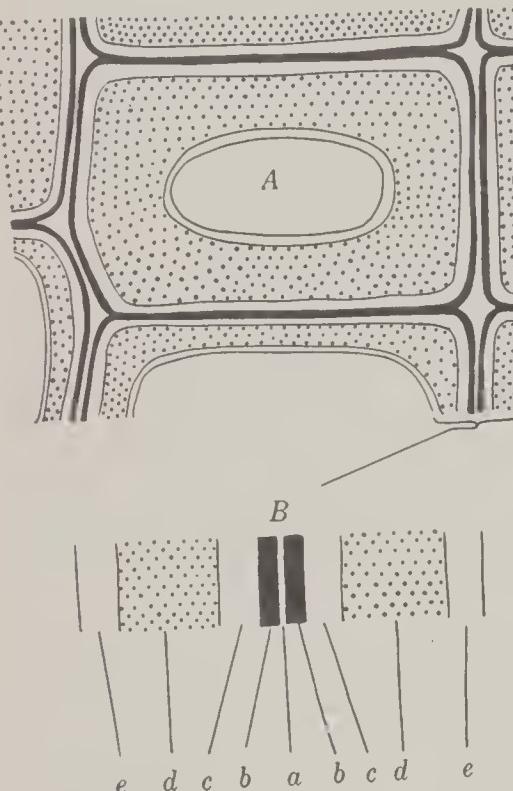


FIG. 2. A, diagrammatic transection of one entire tracheid and parts of seven others; B, section of adjacent walls more highly magnified: a, truly isotropic intercellular substance; b, cambial or primary wall; c, outer layer of secondary wall; d, central layer of secondary wall; e, inner layer of secondary wall. (Redrawn from Kerr and Bailey, *Jour. Arnold Arb.*)

intercellular movements and adjustments that are necessary in the development of cambial or meristematic derivatives.

Recently, Bailey (4) has reemphasized the necessity of critical cell wall analysis, stating that "in any discussion of the higher plants, it is essential to differentiate accurately and consistently between three distinct categories of structures." These are: (1) the *meristematic, embryonic, or cambial* cells and derivatives of them which have retained their capacity for growth and increase in

volume by expanding and increasing the surface area of the *primary wall*, and are further characterized by their potentiality to undergo reversible changes in thickness, etc.; (2) the *fibers*, and other highly specialized cells, which have lost the above potentialities owing to irreversible changes; and, in addition to the primary wall, which may be more or less specialized, have a supplementary or *secondary wall* which is primarily mechanical in function and incapable of growth or increase in surface area; and (3) the inter-cellular layer referred to above as the *intercellular substance* or *middle lamella*.

PRIMARY WALL FORMATION. — The first step in wall formation is the development of the *cell plate*, which occurs in the equatorial plane of the spindle during the later phases of nuclear division. One theory of cell plate formation is that it is derived from the materials of the spindle, and that the plate subsequently splits to form two plasma membranes, which in turn secrete the pectic substances of the middle lamella. An alternative theory is that the cell plate zone may be a more fluid layer resulting from the formation of two dissociated protoplasmic phases, one of which forms the cell plate region and the other the plasma membranes which secrete the pectic materials into the fluid layer. More investigation is needed on this point, but the concept of a fluid cell plate zone is not out of harmony with the process of cell division by furrowing such as occurs in the formation of the microspores of many of the higher plants (*Nicotiana*, *Medicago*, *Melilotus*, *Lactuca*, etc.) as well as in lower plant forms. In the microspore mother cell, the furrows are initiated at the periphery and develop centripetally in contrast to the formation of the cell plate from the spindle, which is usually centrifugal.

The primary wall, which consists of an anisotropic layer of cellulose and pectic materials, keeps pace with the enlargement of the protoplast by stretching and by the addition of new wall substances by intussusception or apposition. In the former, the addition of materials is carried on through a process of infiltration in which additional substances are introduced among the older ones; while in the latter there is a centripetal deposition of additional wall substance which forms thin plates or lamellae against the original wall. It seems probable that in many instances, the thickening of the wall is accomplished by the joint operation of both processes.

SECONDARY WALL THICKENING. — As the cell differentiates, its walls may be variously thickened and additional layers are deposited against the primary wall. Bailey and Kerr (5) have described the secondary wall of normal tracheids, fiber-tracheids, and libriform fibers as consisting of three layers: narrow outer and inner layers, and an intervening one of variable thickness. (Fig. 2.) The outer and inner layers differ from the middle one in the orientation of the cellulose fibrils, which are arranged at approximate right angles to the long axis of the cell, while those of the middle layer are longitudinally or diagonally parallel to it. They find, however, that deviations from the "typical 3-layered type of secondary wall are not of infrequent occurrence." In many thick-walled fibers, there appears to be no differentiation of the inner layer; and the middle layer may consist of a series of lamellae or growth rings. Kerr (24) has shown for *Gossypium* that each growth ring is comprised of two lamellae, one porous and the other compact, and that one of these double rings is deposited daily. (Fig. 3.)



FIG. 3. Transection of a cotton fiber grown under field conditions, swollen in cuprammonia, and subjected to pressure to show the conspicuous pattern of the growth rings. $\times 550$. (Photomicrograph by Anderson and Moore, *Ind. and Eng. Chem.*)

THE PITS. — The pits are thin spots in the cell wall which occur at points where no secondary wall materials have been deposited. In the formation of the secondary walls of two adjacent cells, the wall substance is laid down in such a way that these spots coincide, being separated only by the pit membrane consisting of the two primary walls and the intercellular substance. A *simple pit* is comprised of two opposed cavities with straight sides, which are separated by a closing membrane; but such pits may be variously modified with respect to size and shape, and their frequency and distribution depend upon the nature of the tissue of which the cell is a component part. In some instances, the secondary walls bounding the pit project inwardly without contacting the membrane and overarch the cavity to form a *bordered pit*. In such types, the central portion of the primary wall or pit membrane may be thickened

to form a *torus*. The bordered pit is found chiefly in the walls of the vascular elements of secondary xylem; and, where these abut parenchymatous cells, the pit may be bordered in the wall of the vascular element and simple in the wall of the parenchymatous cell, thus forming a *half-bordered pit*. Other types of secondary thickening found in vascular elements, including the annular, spiral, scalariform, and reticulate types, are described under xylem tissue.

STRUCTURE OF THE CELL WALL. — The detailed structure of the cell wall has been investigated by a number of methods, including X-ray analysis, differential staining, chemical and ash analyses, polarized light, microscopic observation of both treated and untreated materials, and hydration and swelling of the wall with various reagents. As a result, several concepts of the wall structure have been proposed, which are here summarized.

The oldest idea, and one which still receives widespread support, is the hypothesis proposed by Nägeli (30). According to this concept, the cellulose portion of the wall consists of elongated, crystalline, submicroscopic units known as *micelles*, which are separated from one another by colloidal materials. On the basis of X-ray analysis, it is thought that the micelle consists of cellulose groups made up of parallel chains of glucose residues to which varying lengths and numbers of glucose units have been assigned by different investigators.

Sponsler (41, 42) has proposed a second idea of the structure of the wall in which the cellulose units form a three-dimensional space lattice; and has demonstrated that the molecules are arranged in parallel layers, some of which extend lengthwise of the fibers while others are at right angles or otherwise oriented at definitely determined angles. The X-ray patterns and other data indicate "that the units are attached in chains of indefinite length"; and the lattice concept of wall structure does not necessitate the assumption of "the existence of micellae as *structural units of the cell wall*, that is, large units made up of many molecules, such as Nägeli proposed."

A third theory presupposes the existence of larger, visible cellulose units, which have been called by various names: fibrils, cellulose units, ellipsoid bodies, dermatosomes, etc. This idea has been supported by Lüdtke (28), who described the units as being enclosed by thin films of non-cellulose cementing material

which may vary in chemical constitution in different walls. Farr and Eckerson (17) state that the ellipsoid bodies in *Gossypium* are jacketed by a pectic cement, and Farr and Sisson (18) suggest that these visible units satisfactorily account for the X-ray patterns that have been ascribed to the existence of micellar units. This view is not supported by Bailey and Kerr (5), who object to the size of the ellipsoid bodies on the ground that they would exceed the width of more than four lamellae in the cotton fiber. Anderson and Kerr (2) raise additional objections relative to the cementing substances of pectic material which are described as surrounding the ellipsoidal particles, the migration of these particles into the wall through the selectivity of the permeable membrane, and the orientation of the particles in the wall.

CHEMISTRY OF THE CELL WALL. — The chemical composition of the cell wall varies with the age of the cell and with the type into which it ultimately differentiates. In the initial stages of development, the middle lamella is made up chiefly of pectose with small amounts of cellulose. As the cell attains its full size the pectose rapidly forms an insoluble pectate, commonly calcium pectate, thus making the wall more firm and resistant. The continued deposition of pectose and increasing amounts of cellulose, as well as some hemicelluloses, results in the formation of the primary wall, while the secondary wall is at first composed almost entirely of cellulose and some hemicelluloses, but no appreciable amount of pectic compounds. In parenchymatous cells, this condition may obtain throughout the life of the cell; but, in other tissues, the wall may be further modified by lignification, cutinization, or suberization.

In lignification, the lignin, which is an amorphous substance, first appears in the middle lamella; and, although it has been suggested that the pectic substances of this zone are converted into lignin, the investigations of Kerr and Bailey (25) and of Harlow (22) indicate that they are still present even in heavily lignified middle lamellae. The primary wall may be lignified and also the secondary one, but it seems probable that there is more than one type of lignin involved. The addition of lignin may increase the mechanical strength of the cell wall without affecting its permeability to any great extent; but, when the wall is infiltrated with cutin or suberin, it becomes relatively impermeable to liquids or gases.

Suberization occurs in connection with the maturation of the walls of cork cells, phellem. Priestley and Woffenden (34) have considered the causal factors in cork formation and report that there is first a blocking of the parenchymatous surface, which usually is accomplished by the deposition of suberin or cutin in the presence of air. This is followed by an accumulation of sap at the blocked parenchymatous surface and the development of an active phellogen in the parenchyma.

In cutinization, the cutin may be deposited in all the walls of the epidermal cell, or on the inner face of the outer epidermal wall; but, most frequently, it is laid down on the outer surface of this wall, forming a protective non-cellular membrane known as the *cuticle*, which forms an impervious layer except where there are stomata. The cuticle is variable in thickness, being well developed on the epidermis of ripe fruits and the vegetative organs of many xerophytic plants.

Other chemical changes may occur in the epidermal walls of some seed coats. In Linum, they become mucilaginous, as a result of modifications of the pectic substances and cellulose of the wall; and their capacity to hold water is greatly increased. Under certain circumstances, mineral substances, carbonates, oxalates, or silicates are deposited in cell walls. Silicates occur in relatively large quantities in the peripheral cells of the stems of the grasses, and an extreme case of mineralization takes place in the development of cystoliths in the epidermal cells of Cannabis.

TISSUES

Strictly defined, a *tissue* is a group of cells of common origin having essentially the same structure and performing the same functions. Usage has broadened the scope of the term, however, so that now it is necessary to refer to *simple tissues*, which conform to this definition; and *complex tissues*, aggregations of simple tissues, that have come to be regarded as having structural or functional unity. This extension of the term to include complex tissues such as xylem and phloem is convenient in descriptive anatomy, but it should be noted that they refer to vascular complexes consisting, in some instances, of four or more distinct cell types rather than a single one. The tissue concept is further complicated by duplication and lack of uniformity in the usage of terms, the nomenclature used depending upon whether the point of view is

anatomical or physiological. For example, where the classification is based upon function, conducting tissues have been called the *mestome* and protective tissues the *stereome*. The mestome has been further divided into the *hadrome*, conducting water and substances in solution; and the *leptome*, comprised of food-conducting tissues. Since these terms are not the morphological equivalents of such designations as sclerenchyma, xylem, and phloem, their use in

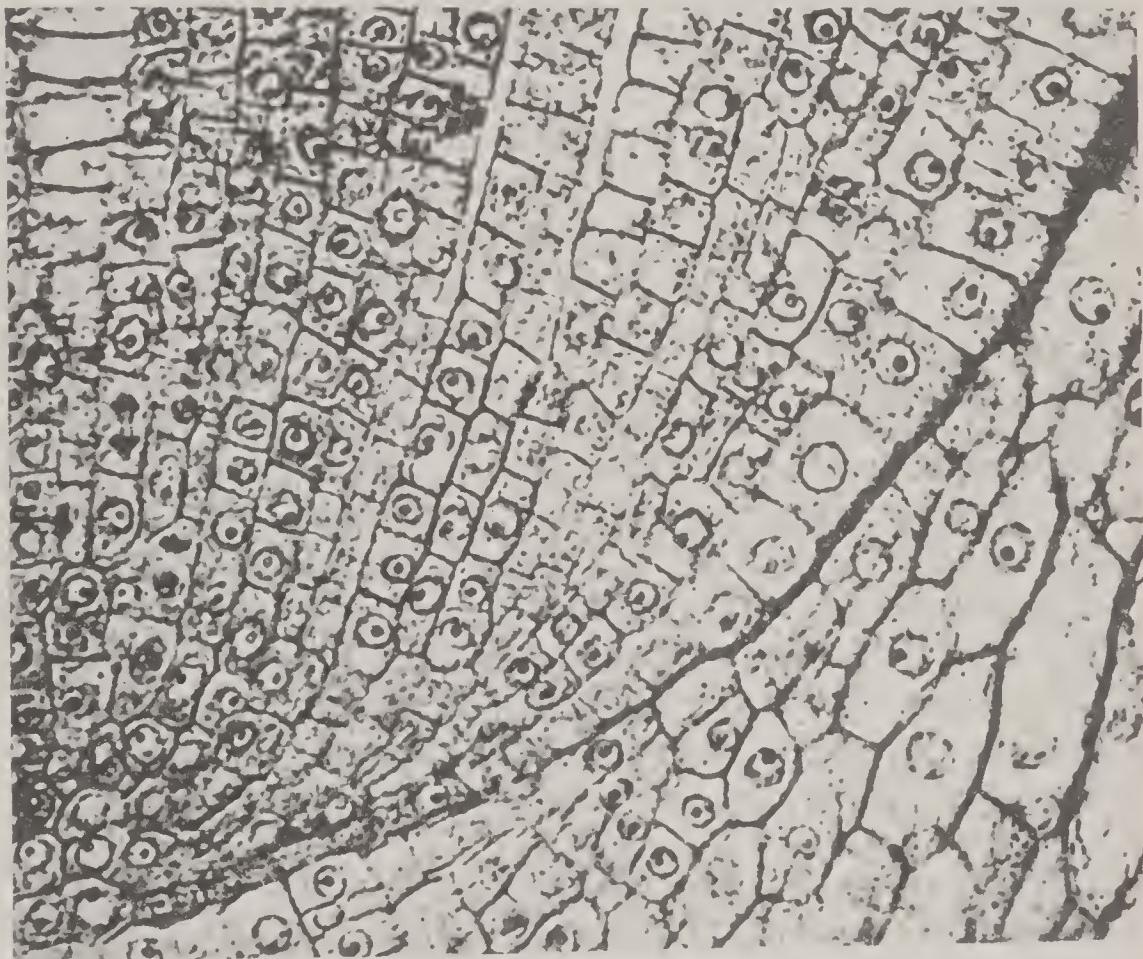


FIG. 4. A quadrant of the root tip of corn illustrating the progressive differentiation of meristematic cells to form vessel segments, parenchymatous cells, epidermis, and root cap.

anatomical descriptions may result in confusion, and they are not used in the succeeding chapters.

MERISTEMS. — All the potentialities for development which are ultimately expressed in the mature seed plant reside in the *fertilized egg* or *zygote*; and, in the embryo derived from it, these are transmitted by the actively dividing nuclei of the cells which form the *terminal*, *intercalary*, and *lateral meristems* of the axis. (Fig. 4.) In developmental anatomy, tissues may be further classified as being actively meristematic, potentially meristematic, or non-meristematic. Active meristems are cell aggregates constituting

the genetic or formative tissue, in contrast to those which retain this quality but seldom express it except under unusual circumstances (potential meristems), or which have no capacity for further growth and differentiation (non-meristems). The cells in meristematic regions are characterized by their approximate isodiametric form, except for some of the cambial initials of lateral meristems; the presence of a functional protoplast which is capable of active nuclear and cellular division; and a primary wall that may grow and enlarge or undergo reversible changes in thickness. The wall is composed largely of cellulose and possesses plasmodesma in varying degrees of frequency and aggregation.

FACTORS OF DIFFERENTIATION. — The tissues which form the complex structure of the plant are derived from the meristems, but the causes which underlie differentiation and the factors which control the processes concerned in it are still incompletely understood. Geneticists have provided a theoretical unit of heredity in the *gene*, and the transmission of heritable characters from one cell generation to another through nuclear division has been shown to be related to this remarkably regular and normally precise process. This aids in the understanding of many of the phenomena of vegetative reproduction, and variation in nuclear behavior may explain some of the problems of mutation and variation in the species; but it is yet to be determined why two adjacent cells of common origin, and presumably with the same hereditary pattern, should differentiate into elements that appear totally unlike each other in structure and function. The factors which are responsible for this differentiation may lie partly within the cell; but undoubtedly the mechanical, physical, and chemical stimuli of the surrounding environment play an important part in the process.

In this connection, continued work with tissues and organs in culture such as that initiated by Robbins (36), White (44), LaRue (27), and Bonner (8) should increase our knowledge of the factors involved in differentiation. Recent work by Went and Thimann (43), Kraus and his coworkers (26), Boysen-Jensen (10), and others on *phytohormones* and their relation to growth and development offers an additional avenue of information regarding this subject.

It seems probable that the positional relationships of cells may play some part in the character of their differentiation. Seeliger (39) points out in his study of sugar beets that "in the development of supernumerary tissues it is not the morphological

origin of a cell but its topographic relation to the axis and the neighboring tissues which determines its future." Priestley and Swingle (33), in their work on vegetative propagation, reach somewhat the same conclusion.

PARENCHYMA — POTENTIAL MERISTEM. — The fundamental parenchyma occurring in various organs of the plant may be regarded as potentially meristematic in contrast to the active meristems; and, as long as these cells retain their functional protoplasts, they also have the capacity for further development and differentiation which may or may not be expressed later. This characteristic of parenchyma explains the origin of many of the anomalous or adventitious structures that arise in the later development of the plant body. Some of the parenchymatous cells may achieve maturity without further differentiation except for an increase in cell size and wall thickness. Such cells form the fundamental ground tissue which constitutes, at least in part, the pith, cortex, and rays of the stem axis; the cortical region of the root and the pith when present; and the mesophyll. In the leaf, the parenchyma is often characterized by the presence of chloroplasts and is referred to as chlorenchyma; but, in addition to the photosynthetic function, these cells store food for short or relatively long periods.

Where no potentialities are expressed, the parenchymatous cell may maintain itself as such throughout the major portion of the life of the plant; and, in some woody perennials, the cells of the ray tissue remain alive for many years. In other cases, they gradually become necrotic; or they may disintegrate early in ontogeny so that lysigenous or schizogenous cavities occur. The hollow medullary cavity frequently found in mature herbaceous stems such as *Triticum* and *Cucurbita*, the large lacunae in the vascular bundles of *Zea*, and those in the cortex of the stem of *Pisum* are formed in this manner.

THE PERICYCLE. — The pericycle is the peripheral layer of the stele, and may be regarded as a potential meristem. In the early ontogeny of the axis, it commonly consists of a single layer of parenchymatous cells lying immediately centrad to the endodermis. The pericyclic cells have no morphological characteristics which distinguish them from other parenchymatous cells; and were it not for their special relation to the stele and the variety of ultimate cell types that may be derived from them, they would not

require separate consideration. In root axes, a very common development is for the pericyclic cells to continue active division in both radial and tangential planes so that the pericyclic zone increases in width and maintains its continuity circumferentially as secondary thickening occurs in the stele. The individual cells also tend to enlarge tangentially and frequently serve for storage. In stem axes, the pericyclic zone may also be broad; but, in the absence of a clearly marked endodermis, its outer limits are often difficult to define since the pericyclic cells may resemble structurally those of the cortex or phloem.

Other tissues that frequently develop from the pericycle are the protective periderm and fibers which are described in succeeding sections under their appropriate functional classifications. Another important pericyclic function is its capacity to produce lateral and adventitious roots and shoots. Other less common potentialities include the production of secondary cambiums (*Beta*), the development of oil ducts (*Apium* and *Pastinaca*), and the formation of glands, lactiferous cells, and canals.

PROTECTIVE AND ABSORPTIVE TISSUES

The superficial protective or absorptive tissues of the plant may be differentiated early in ontogeny, as is the *epidermis*; or they may arise later in development, as in the formation of cork tissue or *phellem*.

THE EPIDERMIS. — The epidermis serves for protection, or, in some regions, for absorption and secretion; and the entire outer surface, with the exception of certain protected growing points, is covered by a single layer of epidermal cells which is continuous except where it is interrupted by stomatal or lenticular openings. Although it is usually one layer in thickness, the cells may divide periclinally to form a double or multiple layer as in *Solanum tuberosum*, where an ephemeral periderm develops from the epidermis early in the ontogeny of the tuber. The epidermal cells may vary greatly in size and shape; but they are typically flattened parallel to the surface, and square or rectangular in transection with the free surface exhibiting more or less convexity. In surface view, they may be tabular or platelike; but frequently the walls are undulating or sinuous, with lobes or projecting angles.

The cells contain cytoplasm and a nucleus, the former usually occupying the periphery of the cell surrounding a large central

vacuole. Chloroplasts are commonly absent except in specialized guard cells. The walls may be unequally thickened, the outer one in most cases being the thickest, while the radial walls are frequently thicker than the inner one.

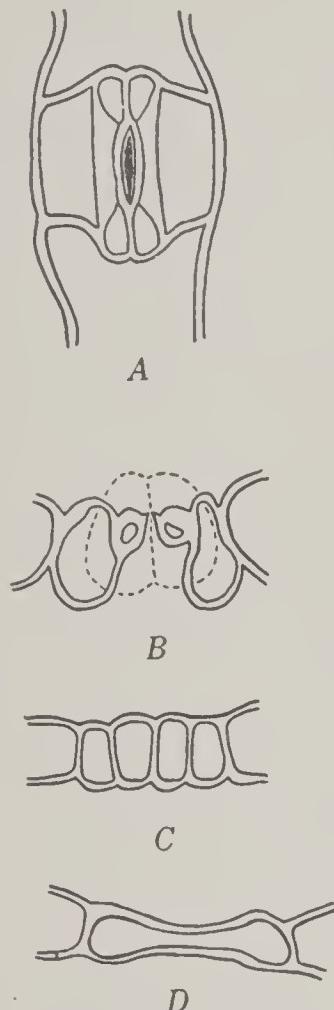


FIG. 5. A, surface view of the stoma of wheat showing guard cells and accessory cells; B, median transection of same; C, transection across one end; D, longisection of a guard cell. (Redrawn from Percival, *The Wheat Plant*, Duckworth and Co.)

THE STOMATA. — The distribution and number of stomata vary with the species, and also with the organ of the plant. In general, they are more abundant on leaves than on stems; and, in the former, more numerous on the adaxial surface than on the abaxial; although, in some instances, as in the grasses, they occur in approximately equal frequency on the two surfaces. The *stoma* is a slit-like opening in the epidermal layer which permits movement of gases between the outer atmosphere and the intercellular spaces of the mesophyll. It is bounded by a pair of *guard cells* with concave facing surfaces and contiguous end walls; and the size and shape of the stomatal aperture is determined by the guard cells, and *accessory cells* when present, varying with changes in their turgidity. The guard cells may have characteristic wall thickenings that are correlated with their turgor movements. In some cases, the walls are uniformly thickened and the guard cell appears round or elliptical in transection; but, more frequently, each guard cell has two parallel ridges on its concave surface which form protruding flange-like margins bordering the outer and inner limits of the aperture. The outer ridge is generally more prominent than the inner, which may be lacking. (Fig. 5, B.)

The position of the guard cells in relation to the outer surface of the epidermis is variable. In *Allium*, the level of the guard cells does not equal that of the epidermis; and they are somewhat depressed, forming a cavity which may be overarched by the adjacent epidermal cells. In *Ipomoea*, *Solanum*, and *Zea* the guard cells, though smaller than the epidermal cells, are so oriented that they project slightly above the epidermal surface; while

in *Lactuca*, the guard cells and epidermal cells are equal in height.

In the development of a stoma, the dermatogen cell which is to produce it usually divides into two unequal daughter cells, one of which becomes the *initial cell* of the stoma and the other an epidermal cell. Then the initial cell, which may be designated as the *stomatal mother cell*, is bisected by an anticlinal wall, the two daughter cells becoming the guard cells. This usually occurs in young epidermal cells shortly after they have been cut off by the dermatogen; but the formation of stomata in a given region does not occur simultaneously, and a progressive series of developmental stages may frequently lie in close proximity to one another.

De Bary (7) has described three distinct types of stomatal development, which are here briefly summarized. In type (1), as in *Allium*, the *initial cell* is the *stomatal mother cell* which divides to form the two guard cells, their opposing walls separating schizogenously to form the stomatal opening. In type (2), as in the first, the *initial cell* is the *mother cell* of the stoma; but, shortly after it is differentiated, *accessory cells* are cut off from the adjacent epidermal cells and run nearly parallel to the guard cells. This type occurs in most Gramineae, including *Zea* and *Triticum*. (Fig. 5.) In type (3), the *initial cell* is not the *mother cell* of the stoma, but undergoes one to several successive divisions which result in the formation of the *mother cell* and one or more *accessory cells*. The manner in which the initial cell is divided and the new cell walls are laid down is variable; but a common sequence is found in *Raphanus*, where the new anticlinal walls are formed successively in three directions and cut off a series of accessory cells which surround the mother cell. Other examples of this type occur in *Apium*, *Ipomoea*, and many of the Solanaceae. (Fig. 6.)

EPIDERMAL HAIRS. — The epidermal cells may form directly or give rise by division to various types of absorptive, protective, glandular, or non-glandular hairs. These may be conical and pointed, globular and capitate, unicellular or multicellular, and unbranched or variously branched.

ROOT HAIRS. — In root tips, the epidermal cells immediately above the zone of elongation develop as root hairs by the extension of the outer wall to form an elongated tube. The hair first appears as a rounded protuberance involving the whole or a part of the outer wall; and, by rapid elongation, develops into a unicellular

tubular structure with thin cellulose walls. The cytoplasm forms a thin layer immediately within the wall, and the nucleus may frequently be located in the extended portion of the cell. With few exceptions, the hairs are short-lived, soon collapse, and the basal portion may become suberized or lignified. New hairs are formed continuously so that a definite zone of root hairs is maintained directly back of the elongating portion of the root axis.

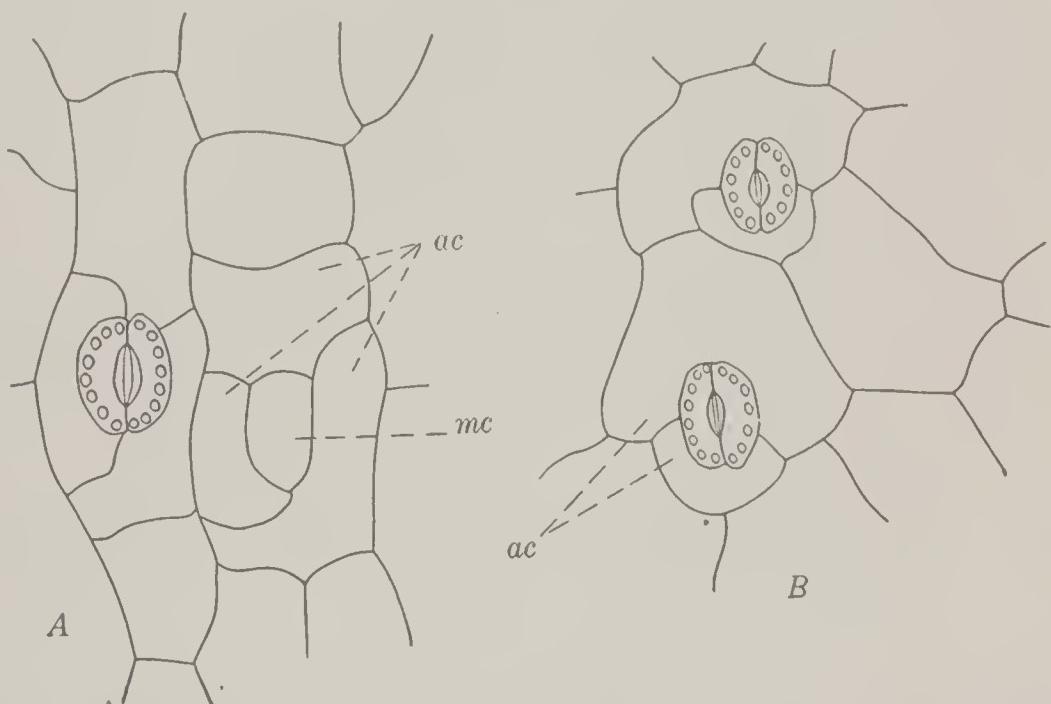


FIG. 6. *A*, a portion of the epidermis of the celery petiole showing a stage in the development of the stoma; *B*, the epidermis of the blade showing stomata, guard and accessory cells: *ac*, accessory cells; *mc*, mother cell.

SHOOT HAIRS. — The numerous epidermal hairs produced on the stem, leaf, and inflorescence are variable as to form and structure. In many instances, they appear to have little functional significance, but the abundant production of hairs on the exposed surfaces of aerial organs does result in a pubescence which may be protective. Characteristic glandular hairs are developed in *Cannabis* and *Lycopersicum*; and, in *Lactuca*, stigmatic hairs occur which are related to the process of pollination. Many plants, including *Cucurbita* and *Solanum*, have multicellular hairs which may or may not be capitate, and unicellular hairs are common in *Medicago* and *Cannabis*. A type of special economic interest is the fibrous hair which develops from cells of the epidermis of the ovule in *Gossypium*. (Chapter XIV, Fig. 227.)

THE PERIDERM. — In both root and stem, there may be derived from the pericycle a *phellogen* or cork cambium whose derivatives mature as a *periderm* that serves as a protective tissue following the loss of the epidermis and cortex. Normally, the cells of the phellogen, derived from the outer pericyclic cells, undergo tangential divisions similar to those of a true cambium, differentiating as *phellem* (cork cells) centrifugally, and *phellodermal cells*, centripetally; but the production of phellem and phellogerm is not necessarily reciprocal. Frequently, the number of layers of cork cells cut off greatly exceeds the production of phellodermal layers; and, in some cases, the activity of the phellogen may be unilateral so that only cork cells are produced. The phellodermal cells and the parenchymatous cells of the pericycle centrad to them form a zone which has unfortunately been referred to as a secondary cortex because of its functional and structural similarity to the true cortex. This terminology is misleading, since it implies a cortical rather than a stelar origin of these tissues; and, where such a zone is formed, it is less confusing to denote it as a pericyclic region, or as secondary parenchyma in cases where the pericyclic and phloem tissues cannot be accurately delimited.

Although the phellogen is commonly derived from pericyclic tissue, this is not always the case. In the young tuber of *Solanum* an ephemeral phellogen may arise in the epidermis which is soon replaced by one of cortical origin. In herbaceous and young woody stems, the initial phellogen very frequently forms in the subepidermal layers of cortical parenchyma; while, in older woody axes, the cork cambium develops from secondary phloem parenchyma.

THE ENDODERMIS. — The functional significance of the *endodermis* in roots is a matter involving much difference of opinion, and several theories have been advanced which have some experimental confirmation. The presence of the *Casparyan strip* makes the radial and end walls relatively impervious to the diffusion of water. This suggests that the endodermis may act as a controlling factor in the lateral diffusion of substances between the cortex and stele, since it restricts the passage of material to the protoplast with its semi-permeable and limiting membranes rather than affording free diffusion through the walls. The presence of *passage cells* in cases where the endodermis develops to the tertiary stage may be regarded as supporting evidence for this theory. (Fig. 7.) Priestley and North (31) have proposed that the endodermis may

also serve to maintain pressure relations in the stele and prevent the accumulation of air in the conductive tissues. Schwendener (37) has proposed that the primary function is that of mechanical support and protection to the stele when the outer cortical cells are lost. The presence of abundant quantities of starch in the endodermis of the stem in some plants suggests that storage may be an important function. In *Linum*, *Cucurbita*, and others, the endodermal layer may be involved in the initial stages of lateral root development, forming a part of the root cap.

The endodermis is a relatively restricted tissue constituting the inner limit of the cortex and lying adjacent to the stele. It

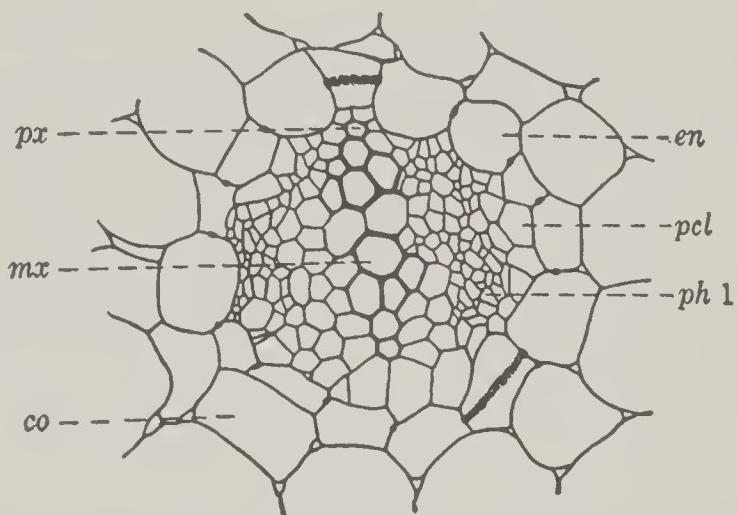


FIG. 7. Transection of a young primary root of potato showing Casparyan thickenings on the endodermal walls: *co*, cortex; *en*, endodermis; *mx*, metaxylem; *pcl*, pericycle; *ph 1*, primary phloem; *px*, protoxylem.

is usually a single layer in thickness, but an exception has long been known in the root of *Brassica oleracea*, reported by Woronin (46), in which a double endodermis may develop. Other exceptions occur in *Lactuca*, in which single cells or sectors of the endodermis may undergo tangential division; and in *Cynara Scolymus*, where it becomes two-layered early in ontogeny.

The endodermal cells form a compact layer which is uninterrupted by intercellular spaces. In transection, they are four-sided, oval, or elliptical, and more or less extended in the tangential direction; while, in the vertical plane, they are elongated with end walls that are usually transverse. The cells retain their protoplasts and possess all the potentialities of typical parenchyma, including the capacity for cell growth and division. The nucleus is prominent, and the cytoplasm frequently contains starch grains in such large

numbers, as compared with the adjacent pericyclic and cortical cells, that the term *starch sheath* has been applied to the layer. In addition to starch, other substances such as tannin, mucilage, and occasionally crystals may be present.

The structure of the cell wall is the outstanding feature of this tissue in cases where Casparyan thickenings are laid down. The endodermal cells are at first uniformly thin-walled and parenchymatous with no characteristics which might distinguish them from adjacent cells. In the early development of the root, thickenings are laid down on the radial and end walls which consist of strips of wall material deposited on the primary wall. The strips are suberized or cutinized and as seen in transection (in this view referred to as Casparyan dots), may appear to consist of a central core of cellulose and pectic substances covered by a layer of suberin or cutin. It is also possible that the water-proofing substances may infiltrate into the primary wall to some degree; but, in any event, the effect is to allow water and solutes to pass through the protoplasts and tangential walls of the endodermal cells, and to greatly restrict the movement through the radial and end walls. The width of the strip is variable, being very narrow in some cases so that in transection it appears as a rounded or oval dot; while in others it may equal the width of the whole radial wall, which then appears in transectional view to be more or less spindle-shaped. At this stage, according to Eames and MacDaniels (15), the tangential walls consist of relatively thin cellulose with few, if any, pits. Simple pits which extend through the Casparyan strip when it is wide occur in the radial walls and there are some pits in the end walls.

The endodermis frequently remains in this secondary stage of development without further modification; but there may be a tertiary phase in which additional secondary wall thickening occurs involving the inner tangential, radial, and end walls and occasionally the outer tangential wall. These walls are sometimes much thickened and lignified, the size of the cell cavity being very greatly reduced. In roots where tertiary development occurs, certain cells usually opposite the protoxylem points may remain in the secondary condition and are referred to as *passage* or *transfusion cells*. In this stage, the endodermis has no further capacity for division and growth; and, if the axis continues to enlarge, its cells are ultimately ruptured, together with the structures outside it.

An endodermis of this type, in either the secondary or tertiary stage, is frequently found in roots, underground stems, and the stems of hydrophytic plants. In the aerial portions of the axis of herbaceous plants, the endodermis generally remains in the primary condition without developing Caspary strips; and, if it differs from the adjacent tissues at all, it is in the greater starch content of its cells, in their shape or size, and in the uninterrupted continuity of the layer.

MECHANICAL TISSUES

The tissues which give strength, and those that provide toughness combined with elasticity and flexibility, constitute the mechanical elements of the plant body. These include *collenchyma*, *non-sclerotic fibers*, *sclerenchyma*, and the *lignified elements* of the vascular system. The sclerenchyma may consist of elongated *sclerotic fibers* or approximately isodiametric *stone cells*.

COLLENCHYMA. — This simple tissue has many characteristics of parenchyma and may be regarded as a derived form of it. The cells retain their protoplasts at maturity, are capable of further division, and differ from parenchyma chiefly in the manner in which the walls are thickened. The cells are axially elongated, rounded, or more frequently angular, and four- to six-sided in transection, with end walls that are straight, oblique, or tapering. The elastic walls have simple pits, are readily permeable to water, and are composed chiefly of cellulose although there may be some lignification in old cells. The wall thickenings are laid down in longitudinal strips which are commonly located at the angles of the cells, but the tangential walls, and less frequently the radial walls, may be thickened. (Fig. 241.)

In the stems and petioles of herbaceous plants, collenchyma forms discrete zones or continuous bands of mechanical tissue immediately beneath or near the epidermis. It also occurs in the blade of the leaf, forming strands that parallel the midrib above and sometimes below it. Differentiation of collenchyma begins while the organs are still developing, and it is ordinarily the first type of mechanical tissue to mature in the ontogeny of the stem axis. This may be correlated with the fact that collenchymatous cells retain their capacity to divide and grow which is an essential characteristic for mechanical tissues located in regions that are undergoing elongation.

THE FIBERS.—Fibers occur in the xylem, phloem, pericyclic, and cortical regions of the axis. On the basis of wall structure, they may be divided into *non-sclerotic* and *sclerenchymatous* types, the latter occurring chiefly in the xylem, although the fibers in any zone may become lignified. The non-sclerotic fibers cannot readily be distinguished from one another structurally, and are therefore designated on the basis of their position in the axis and their relation to other tissues. They are sometimes referred to as "bast" fibers in contrast to the wood fibers of the xylem, but the term has been so loosely used that it has little value in descriptive anatomy. It is more accurate to indicate the fiber type by prefixing the name of the region in which it is differentiated, i.e., *cortical fiber*, *phloem fiber*, and *pericyclic fiber*.

NON-SCLEROTIC FIBERS.—Frequently in stems, and not uncommonly in roots, non-sclerotic fibers are differentiated in the pericyclic zone. These may form a continuous cylinder of mechanical tissue, a series of pericyclic masses lying outside the phloem of the vascular bundles, or occur as strands in a discontinuous cylinder. Scattered groups of fibers may also be differentiated in the phloem region and less frequently in the cortex as in *Pisum*. In this type, the walls are non-lignified, or very slightly so, and consist chiefly of cellulose. Where the proportion of cellulose is high (*Linum*) the fiber has remarkable tensile strength and durability coupled with flexibility and elasticity; but, in fibers where some lignification occurs (*Cannabis*) these latter properties are less pronounced and they are more brittle.

In ontogeny, the fiber initial grows rapidly in the axial direction, attaining a length which may be several to many times the original dimension of the cell. In hemp, the average is 3.5 to 4 cm., and fibers 10 cm. in length have been reported; while, in flax, the average is from 2.5 to 3 cm. The extreme length of the fiber is due to the manner of its development. The cell grows without undergoing transverse division as frequently as the adjacent cells, and elongation may continue without cross-wall formation as long as the portion of the axis in which the cell is located continues to grow in length. In addition to this method of fiber elongation, there is probably some sliding action by which the tips of the elongating cells push past one another, thus adding greatly to the mechanical strength of the tissue. This has been termed "gliding growth"; and, although the mechanism of the process is not

clearly understood, it seems likely that it may be accomplished by a splitting or modification of the middle lamella (intercellular substance) which permits the ends of the separated elements to slip past one another.

WOOD FIBERS. — The *wood* or *xylem* fiber is an elongated sclerotic element with tapered ends, which gives mechanical strength and

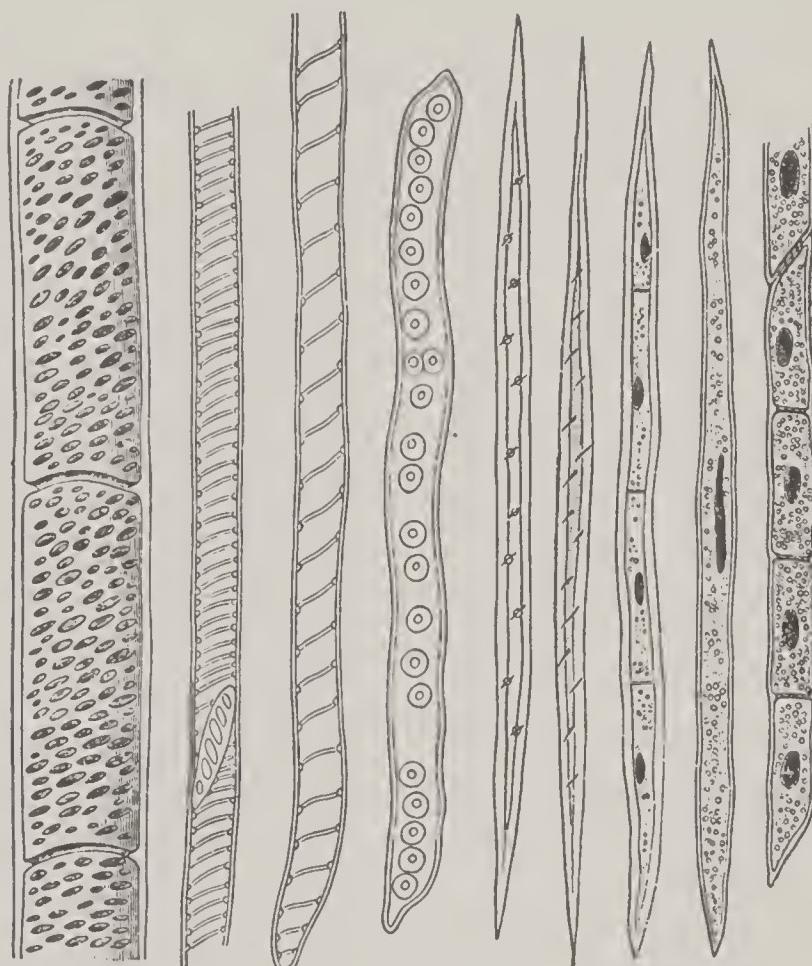


FIG. 8. Tracheae, tracheids, wood-fibers, and xylem parenchyma of a dicotyledon with transition forms between the various elements. Diagrammatic. (From Strasburger, *Textbook of Botany*, Fifth English Ed.)

rigidity to the axis. They vary greatly in form, size, and the chemical properties of the wall; but are usually angular in transection, with thick, heavily lignified walls in which there are bordered pits that may become occluded as the wall thickens. (Fig. 8.) In the development of the wood fiber, the thin-walled, parenchymatous fiber-element grows rapidly, attaining full size before lignification and consequent hardening of the wall occurs. The continued deposition of wall substance results in a reduction in the size of the lumen of the cell, and the protoplast finally dies, leaving

a narrow canal which may be occupied in part by products resulting from the disintegration of the protoplast.

There are intermediate types, representing intergrades between parenchyma and sclerenchyma, in which the elements have relatively thick walls, simple pits, and retain their protoplasts. Such forms are designated as *substitute fibers*. Another intergrading form is the *fiber tracheid*, which exhibits some of the characteristics of the tracheid but functions primarily as a mechanical element.

STONE CELLS. — A second type of sclerenchyma is the *stone cell*, which is frequently short and approximately isodiametric but may vary greatly in shape. The stone cells occur in compact or loosely organized groups as in the fleshy parenchyma of the pear, *Pyrus communis*. They are also common in the hard outer coats of seeds and fruits, as well as in the bark and pericyclic regions of woody stems. There is no sharp distinction between the fiber and the stone cell, and intermediate types of all sizes occur, so that it would be possible to arrange a complete series of sclerenchymatous elements ranging from the isodiametric to the elongated form. The wall of the stone cell is thick, highly lignified, and may be much stratified with clearly distinguishable lamellae. Canals, which are usually branched, occur in the walls, and the continued addition of materials thickens them until, finally, the lumen becomes very small and may be almost completely occluded.

CONDUCTIVE TISSUES

The conductive elements of the vascular plant can be divided into two principal categories, *xylem* and *phloem*, each of which is a complex tissue consisting of an aggregate of four or more cell types. There is also much general conduction through all parenchymatous tissues, especially that of the ray.

THE XYLEM. — The xylem may include *tracheids*, *vessels (tracheae)*, *fibers*, and *parenchyma*; and frequently contains *ducts* or *glands* of various types. Developmentally, it is classified as *primary xylem*, derived directly from the primary meristem; and *secondary xylem*, differentiated from the cambium. The primary xylem is further divided into the *protoxylem*, which is the first to differentiate and mature at a given locus, and the *metaxylem*, which usually matures later. (Figs. 8, 9.)

The spatial relationship of the proto- and metaxylem is important in anatomical diagnosis; and, in the development of the pri-

mary xylem, this is indicated by the terms *exarch*, *mesarch*, or *endarch*. In exarch development, the protoxylem is differentiated at or near the periphery of the stele, usually abutting the pericycle, and the metaxylem is laid down centripetally with respect to it. In the mesarch type, the differentiation of metaxylem proceeds both centripetally and centrifugally from the protoxylem so that it forms a zone on either side of the protoxylem and may completely surround it. In the endarch relation, the protoxylem is differentiated

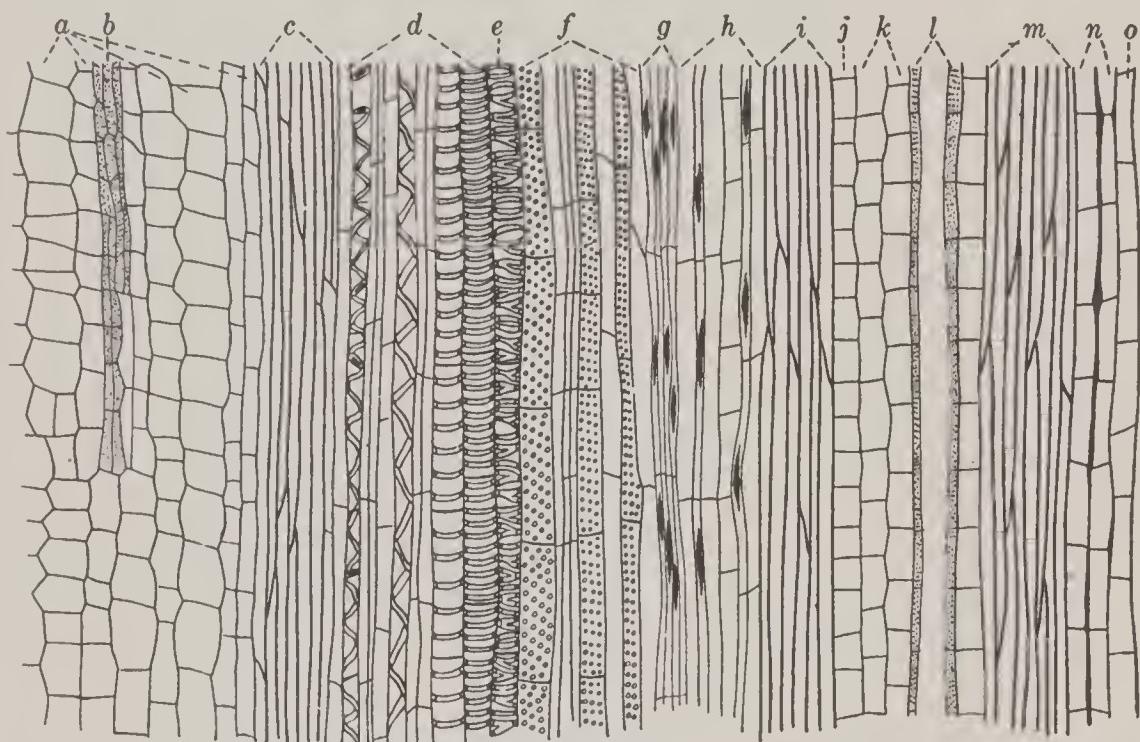


FIG. 9. Longisection of the stem of the parsnip through a bundle: *a*, parenchyma of the pith; *b*, epithelial cells of a medullary oil duct; *c*, mechanical tissue; *d*, protoxylem; *e*, metaxylem; *f*, secondary xylem vessels and parenchyma; *g*, cambium; *h*, sieve tubes, companion cells, and parenchyma; *i*, pericyclic fibers; *j*, endodermis; *k*, cortical parenchyma; *l*, cortical oil duct and its epithelial cells; *m*, collenchyma fibers; *n*, collenchymatous parenchyma; *o*, epidermis.

at or near the center of the axis and the metaxylem is laid down centrifugally. These terms are only used in reference to primary xylem and are not applied to secondary xylem, which is usually laid down centripetally by the cambium.

THE TRACHEIDS. — The *tracheid* is regarded as the basic and, phylogenetically, the most primitive cell type in the xylem tissue. It is angular or roughly four-sided in transection and much elongated with tapered, pointed, or wedge-shaped ends. It is commonly small in transection with a relatively large lumen that is devoid of protoplasm at maturity; and the walls, which are

variously thickened and reinforced, are abundantly pitted, especially at the ends where the cells interlock with one another. The pits are bordered, although in some cases the borders are so narrow that the pits appear to be simple. Thus a vertical series of tracheids forms a conducting strand through which water may move freely.

The character of the secondary wall determines the type of the conducting element. In addition to *pitted* forms, *annular*, *spiral*, *scalariform*, and *reticulate* elements may be differentiated in the primary xylem as a result of the deposition of secondary wall materials in various patterns. (Fig. 8.) The annular and spiral types are most commonly found in the protoxylem. In the former, there is a series of separate ring-like reinforcements, the spacing between adjacent rings depending in part upon the rate and degree of maturity of the element, the rings being farthest apart in the most rapidly growing annular elements because of the vertical elongation of the primary wall between them. In the spiral element, the bands of the secondary wall are arranged in a compact or loosely coiled spiral, the latter condition occurring in protoxylem elements which are differentiated before the elongation of the axis has been completed. It is not uncommon to find transitional forms between these two types in which both spiral and annular thickenings occur.

The scalariform and reticulate elements usually develop in the metaxylem. In the former, the secondary thickenings are laid down in a close series in a ladder-like pattern. The reticulate element has more secondary wall thickening than the scalariform, and the mesh of the network is much finer. Because the proportion of secondary wall material to total wall area is much greater, the scalariform and reticulate elements are more rigid than the annular and spiral types. This affords a good example of structural and functional correlation, since the annular and spiral elements of the protoxylem are commonly differentiated before complete elongation of the axis is accomplished; while the more rigid scalariform and reticulate elements of the metaxylem are usually formed after this has occurred.

THE VESSELS.—The *vessel* consists of a vertical series of cells (*vessel segments*) in which the adjacent end walls are perforated in various ways so that a continuous tube is formed. Frost (20, 21), in discussing the origin of the vessel, points out that it is clearly "a series of individual cells, properly called vessel elements

or vessel segments, which are joined end to end with perforate division walls." The vessel segment may be distinguished from a tracheid in two important respects: (1) it has a definite end wall; and (2) this end wall is perforated in some manner. The perforations may be scalariform-porous, oblique-porous, or transverse-porous; and this sequence represents in a general way the probable phylogenetic order in which the perforations of the end walls of the vessel segments have evolved. The situation in herbaceous dicotyledons is in accord with this generalization; for, in most cases, the vessel segments of the secondary xylem are relatively short, with transverse end walls and perforations of the transverse-porous type. In many angiosperms, the terminal perforation consists of a single large opening; and the end wall may be so completely resorbed that there is no evidence of it except for a slightly projecting ring between adjacent vessel segments. (Fig. 10, C.)

The vessel segment may be narrow and elongated, but frequently the cells are broader than tall. The former condition is common in the loose spiral and annular vessels of the protoxylem, while vessels which are differentiated and matured after the elongation of the axis is complete may have broad segments that are short, cylindrical, and barrel-shaped. Bailey and Tupper (6), in a comprehensive series of measurements of tracheids and vessel segments, found that the former are usually considerably longer than the latter; and that there is a definite correlation between vessel segment length and the character of the perforations. In 276 species of dicotyledons the average vessel segment length was 0.57 mm., while the average length of the tracheids in 146 species of conifers was 3.64 mm. In 274 species of dicotyledons, 168 had transverse-porous perforations; and 138 were 0.3 to 0.6 mm. or less in length. They found further that vessel segments are shorter in the more slowly growing plants; but noted that length is also dependent upon the length of the cambial mother cell and the amount of elongation that the vessel segment undergoes during differentiation. The lateral walls of the vessel segment correspond to those described for the tracheid; and there may be spiral, annular, scalariform, reticulate, and pitted vessel segments.

THE ONTOGENY OF THE VESSEL. — There are several ways in which a vessel may develop, the most common one being that described by Eames and MacDaniels (15), in which the vessel

segments forming the vertical series enlarge in diameter without much increase in length. Until the full size of the vessel is attained, the segments are separated by definite end walls which may lay down some secondary wall thickening. (Fig. 10.) When the segments have attained full size and shape, the dissolution of the end wall begins; and, in the transverse-porous type, the entire end wall disappears, so that a continuous tube results. In *Apium*, Esau (16) found that the ontogeny of the vessel agrees in general

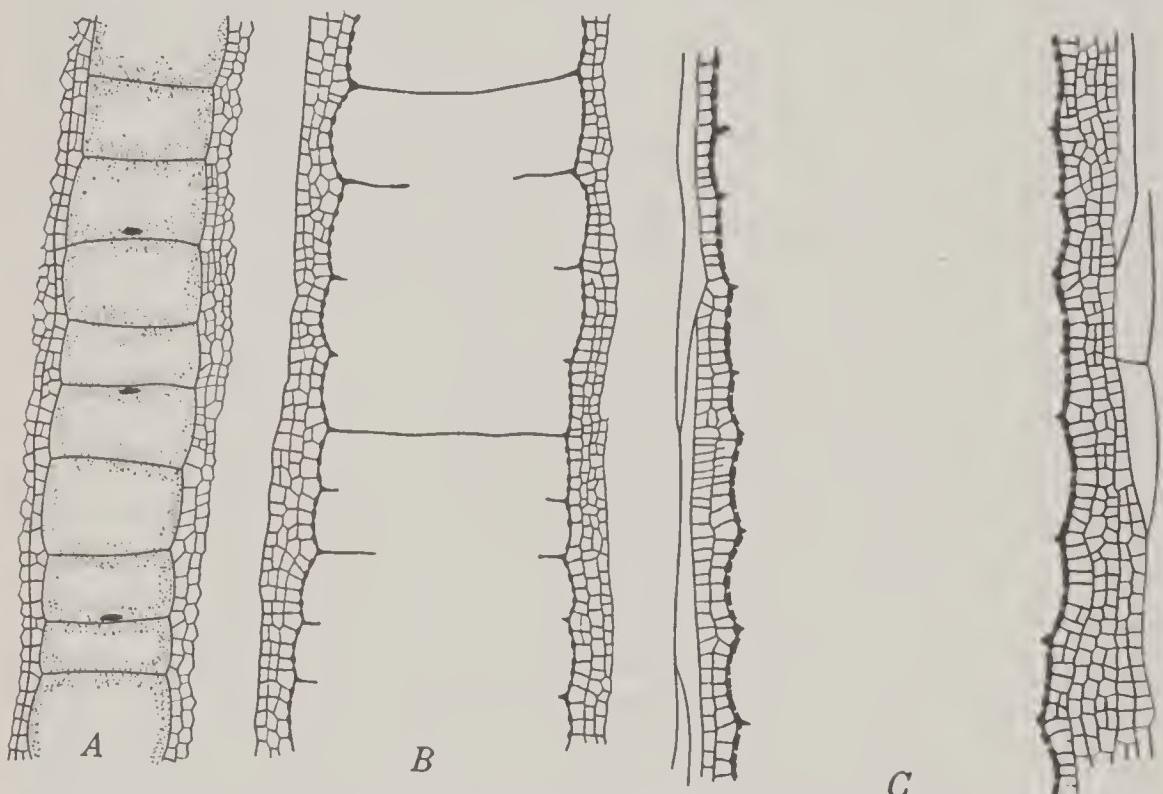


FIG. 10. A-C, successive stages in the ontogeny of the vessel in *Cucurbita* showing the disintegration of the end walls of the vessel segments.

detail with that given above, except that no deposition of secondary wall material occurs on the end walls. The wall thickening appears to be primary and of a peculiar lenticular type somewhat similar to the torus formed in some bordered pits. (See Fig. 244.)

Priestley and his coworkers (32) have described the perforation of the end walls of several species of woody angiosperms as occurring early in the ontogeny of the vessel segment and prior to the initiation of secondary wall thickening; but note that "pectin films are often left stretched across the perforated ends of the vessel segments." They point out that because of these films there is no sudden intermingling of the contents of adjacent vessel segments. Scott (38) has described a coenocytic development of

spiral elements in *Ricinus communis*, in which multinucleate cells are formed from uninucleate procambial cells. After attaining a maximum elongation, a fine spiral of cellulose is laid down throughout the entire length of the vessel; and the development of the spiral and its initial lignification proceed rapidly, keeping pace with the deposition of cellulose. During lignification, the protoplasm of the developing vessel does not appear to disintegrate.

In the later stages of axial development, the thin-walled protoxylem elements may be ruptured owing to the stretching and subsequent collapse of the walls. This frequently occurs with annular elements as in the bundle of *Zea*, where the disintegration of the protoxylem and adjacent parenchyma results in the formation of a large lacuna. In reticulate and pitted vessels, there may be a penetration of the lumen of the vessel segment by the cytoplasm of adjacent parenchymatous cells. This frequently occurs in *Cucurbita* and *Solanum* and results in the formation of *tyloses* which may plug the vessel passage and render it functionless except for the support afforded by its walls. (Fig. 318.)

XYLEM FIBERS. — The structural details of fibers have been discussed, but there is a special relationship existing between the xylem fiber and the tracheid, since both are constituent elements of the complex xylem tissue. The xylem fiber may be regarded as a tracheid which has undergone changes in the course of phylogeny so that it is non-functional as a conductive element, but has increased properties for mechanical support. Because of this, no sharp line can be drawn between xylem fibers and tracheids; and there are intermediate types known as fiber-tracheids. Some of these may have a limited conductive function in addition to their mechanical qualities, since their pits permit some movement of water and substances in solution.

XYLEM PARENCHYMA. — The parenchymatous cells of the xylem which form an important constituent in the xylem complex, especially in many herbaceous angiosperms, do not differ in general characteristics from those described in the section on parenchyma. They are usually arranged in longitudinal rows and may be elongated in the axial direction, except in the xylem rays, where their radial dimension is the greatest. The walls are relatively thin at first, but frequently become thickened and lignified later. The pits are simple in the walls of adjacent parenchymatous cells, while half-bordered pits occur where they abut vessels or tracheids.

In fleshy storage organs, the proportion of xylem parenchyma may be very large as in the root and hypocotyl of Raphanus and Beta; and, in such cases, the cells may remain active and greatly increase in number. In woody axes, xylem parenchyma is limited or may be totally lacking except in the xylem rays. Where secondary thickening occurs, parenchymatous cells cut off by the cambium constitute the *xylem rays*, which may be one to several cell layers in width. The ray appears in a radial longisection as a sheet of tissue, and its height may vary from few to many cells. In herbaceous plants, the xylem ray cells are parenchymatous; but, in woody ones, they may become sclerenchymatous and lignified, eventually forming the most resistant portions of the wood. Unlike the medullary rays, the xylem rays may have no direct contact with the pith, but the latter are in intimate contact with the vertically oriented elements of the stele, functioning in transverse conduction, and serving as a storage region, especially in semi-woody biennials and perennials.

THE PHLOEM. — Like the xylem, the phloem is a complex vascular tissue of the stele. It may include *sieve tubes*, *companion cells*, *fibers*, *parenchyma*, and *secretory cells*; but, frequently, one or more of these elements are lacking.

SIEVE TUBES. — The *sieve tube* is the principal conductive unit of the phloem; but parenchyma is important in this respect, especially in the protophloem, in which sieve tubes may not be differentiated and the elements consist of slender, elongated, parenchymatous cells. Structurally, the sieve tube is a vertical series of elongated, thin-walled cells which are interconnected by perforations in their walls occurring in areas known as *sieve plates*. The end walls may be transverse, oblique, tapered, or beveled; and the sieve plates occur in them, or the lateral walls, or both. Although many angiosperms have lateral plates, there is commonly a single transverse one which is perforated by numerous pores through which the protoplasmic strands extend as continuations of the cytoplasm of the sieve tube segments. It has no nucleus at maturity, but may contain minute starch grains and plastids. Slime bodies have been observed in the cytoplasm of the sieve tubes of many plants, including Beta, Cucurbita, and Solanum; and from the proteinaceous contents of the cytoplasm and cell sap, slime plugs may form which penetrate the pores of the sieve plate.

Hill (23) and others have described the protoplasmic strand as

enclosing a *slime string* of proteinaceous material and being itself surrounded by a *callus sheath* lying between it and the margin of the perforation. Crafts in a series of papers (12, 13, 14) reports that the protoplasmic strands are probably solid, that they do not contain pores through which slime strings extend; and suggests that the "only continuous permeable phase throughout the plant is the cell wall," which "is highly hydrated" in the phloem. He also states that the permeability of the sieve tube increases as the element matures; and that "it seems possible that movement may take place partly through the sieve-tube lumina and partly through the phloem walls."

A development which usually occurs late in the growing season, or late in the ontogeny of the individual sieve tube, is the formation of *callus* on the sieve plate. This at first surrounds the perforation, later may completely cover it; and, in some cases, continues to be deposited until a large mass of callus is formed. Later, it may be dissolved off with a consequent resumption of the activity of the sieve tube; but, in many instances, it forms a permanent layer which terminates the conductive function of the element.

COMPANION CELLS. — The *companion cell* is so named because of its intimate structural and probable functional relationship to the sieve tube. In the ontogeny of the sieve tube and companion cell, the two elements are derived from a common mother cell of the procambial strand in primary phloem, or from a phloem mother cell derived from the cambium in secondary phloem. A longitudinal division of the phloem mother cell divides it into two daughter cells of unequal size, the larger becoming the sieve tube and the smaller the companion cell. The latter contains a very dense protoplast with a distinct nucleus; and is thin-walled, elongated, and triangular, square, or somewhat rounded in transection. The walls adjacent to the sieve tube have numerous simple pits, and there are a smaller number of them in the walls that are in contact with parenchymatous cells. In many herbaceous angiosperms, the length of the companion cell is equal to that of its sieve tube; but the original companion cell may be divided transversely into several shorter cells, so that each sieve tube lies adjacent to a vertical row of two, three, or more short companion cells.

There is variation with respect to the arrangement of the sieve tubes and companion cells. In some instances, the pattern is so regular that the phloem appears in transection as an almost perfect

mosaic, and the relationship between sieve tube and companion cell can be readily determined. On the other hand, there may be much irregularity; and, where there is little difference in the size and shape of the two elements, it is difficult to distinguish one from the other except in longisections where the sieve plates can be observed.

The function of the companion cell is not definitely known; but the fact that the sieve tube and companion cell are intimately connected by plasmodesma, and that the sieve tube lacks an organized nucleus while the companion cell has a conspicuous one, suggests that the companion cell is concerned in some way with the conductive function of the sieve tube.

PHLOEM PARENCHYMA. — The parenchymatous cells of the phloem do not differ histologically from those described under the section devoted to parenchyma, but they may have an important conductive function. This is especially true in protophloem in which sieve tubes are frequently absent and the parenchymatous cells constitute the chief conducting elements. These cells are short-lived and are usually crushed and resorbed as the axis enlarges. The metaphloem also contains some phloem parenchyma, but sieve tubes and companion cells are differentiated.

In the secondary phloem, the proportionate number of parenchymatous cells, sieve tubes, and companion cells is variable, the former being quite abundant in many Compositae and almost completely lacking in some species of Ranunculaceae. Where phloem parenchyma is derived from the cambium, the resultant cells are frequently elongated and tapered, and have been termed *cambiform parenchyma*. In some instances, transverse divisions of these elongated elements result in the formation of a linear series of relatively short isodiametric cells.

Ray parenchyma of the secondary phloem is also cut off by the cambium and the phloem rays often lie on the same radii as the secondary xylem rays, appearing as continuations of the latter outside the cambial ring. At its outer limit, the ray may be funnel-shaped where it widens, owing to continued growth and division of the parenchymatous cells comprising it. The ray cells are commonly elongated in the radial direction, and may remain active over long periods, sometimes through the life of the plant, providing a means of lateral conduction and also a place for storage of food.

PHLOEM FIBERS. — Both primary and secondary phloem fibers occur, which may be non-sclerotic or sclerenchymatous. They are usually arranged in groups or zones, frequently bounding the periphery of the phloem. They also occur as bands which alternate with sieve tubes and companion cells; and, in other cases, they are scattered singly or in small groups throughout the tissue. The thick walls may be somewhat lignified at maturity, differing from those of the xylem fiber chiefly in the presence of simple rather than bordered pits.

SECRETORY TISSUES

GLANDS. — The gland may consist of a single secretory cell, such as the glandular hair in *Cannabis* and *Solanum*; or several cells may form a glandular organ or nectary. These cell aggregates differ in their method of formation and in degree of complexity. Frequently, the gland has a central cavity in which the secreted substance is stored. The cavity may be formed schizogenously by the splitting apart of the walls of adjacent cells and the subsequent formation of a duct by the growth and realignment of the bordering cells. Ducts of this type are termed *schizogenous*, and a common example occurs in the primary oil ducts of the Umbelliferae (*Apium* and *Pastinaca*). (Fig. 11.) In other cases, the formation of the gland or duct may result from the destruction or solution of groups of cells, thus forming a cavity or tube, surrounded by other cells

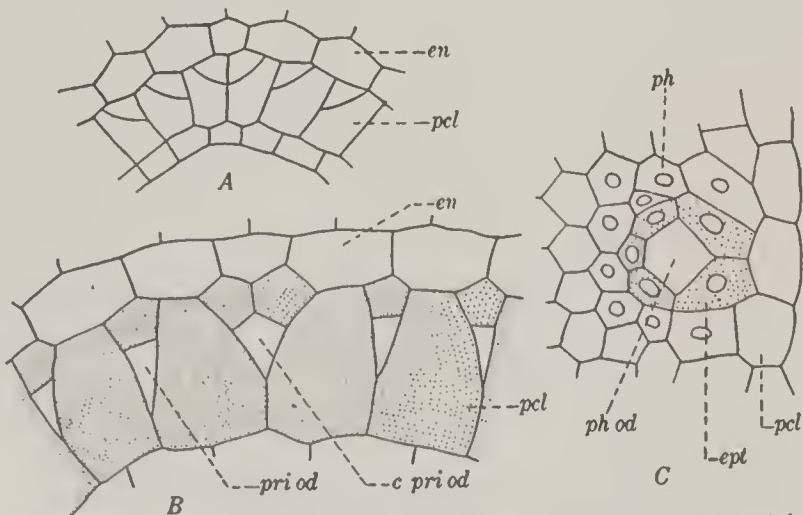


FIG. 11. *A*, sector of the pericycle of the parsnip root showing an initial stage in the formation of the oil ducts; *B*, a later stage in which the oil ducts have been formed; *C*, a section of the primary phloem showing the phloem oil duct: *c pri od*, central primary oil duct; *en*, endodermis; *ept*, epithelial cells; *pcl*, pericycle; *ph*, phloem; *ph od*, phloem oil duct; *pri od*, primary oil duct.

which may remain active or also become dissolved. This type is referred to as *lysigenous*. Lysigenous glands are conspicuous in the leaves and other structures of *Gossypium*, and form the oil sacs of the citrus fruits.

Digestive glands occur in many plants as highly specialized structures or as layers of secretory tissue, especially in fruits and seeds which secrete enzymes that digest reserve foods. This is the case in the grain of *Zea*, where the cotyledon (scutellum) of the embryo is bounded by a layer of digestive cells which forms epithelial glands; and comparable digestive regions occur in the akene of *Lactuca*.

THE NECTARIES. — In plants depending upon insects for pollination, *nectaries* are commonly present. The secretion of nectar is a function of somewhat papillate epidermal cells which vary in their degree of organization and specialization. These cells are not always limited to specific regions constituting a nectary; and may be unspecialized, in which case the secreting cells resemble other epidermal cells except that they have no cuticle. Although nectaries are ordinarily associated with floral structures, extra-floral nectaries may occur as in *Gossypium*, where they develop on the midrib of the leaf and at the bases of the involucral bracts. (See Fig. 224.)

LACTIFEROUS CELLS AND DUCTS. — A special type of secretory tissue, characterized by the presence of *latex*, occurs in several plant families. This substance is a complex emulsion that varies greatly with respect to its chemical constituents. Among other substances, it may contain sugars, oils, proteins, tannins, alkaloids, and gums; and, in addition, starch grains and salts may be present. The viscous fluid is usually milky white (*Lactuca* and *Ipomoea*); but it may be golden brown (*Cannabis*), or less frequently yellow (*Argemone*).

In the Euphorbiaceae, Asclepidaceae, and Apocynaceae, latex may occur in cells which develop in the embryo and finally form a much branched system of tubes. These are morphologically equivalent to a single cell initial which keeps pace with the growth of the apical tissue of the plant. A different type of lactiferous cell is found in the Liliaceae; and, in *Allium*, these appear early in ontogeny in the cortical region of the leaf. They are arranged in longitudinal rows parallel to the epidermis and are interconnected by pits. (See Fig. 92.) A unique form occurs in some spe-

cies of the Moraceae; and, in Cannabis, they develop as unbranched, unicellular vessels which are multinucleate. The vessels originate in young leaves at the tips of the vegetative axis, and develop in the periphery of the primary phloem, attaining an extraordinary length in some instances. Latex vessels of the articulated type in which a longitudinal series of elongated cells coalesce to form a continuous tube occur in Ipomoea and Lactuca. In the latter, the ducts at first consist of a longitudinal series of cells with definite end walls; but, later in ontogeny, they become continuous non-septate passages, and frequent cross-anastomoses result in a system of interconnecting canals. (See Fig. 334.) In both Ipomoea and Lactuca, they develop primarily in the phloem and pericyclic tissues; but, in the latter, they also occur in the cortical region of the axis and the mesophyll of the leaf.

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CHAPTER II

THE ANATOMY OF THE ROOT

THE root is one of the primary organs of the vascular plant. It is typically subterranean, serving in the mechanical support of the aerial portions of the axis, in the absorption and conduction of water and mineral nutrients, and in the storage of reserve foods. In addition to these primary functions, several additional ones may be performed in specific cases, such as the development of adventitious shoots from the fleshy root, the peculiar properties of support and absorption afforded by the aerial roots of certain orchids, and the special nutritional functions performed by many of the roots of the Leguminosae in the symbiotic relations which exist between them and the nitrogen-fixing bacteria of the soil.

Upon germination of the seed, the *primary root* typically grows directly downward, penetrates the soil rapidly, and becomes the initial absorbing and anchoring organ. Other lateral roots may develop in rapid succession. In some plants, especially the Gramineae, embryonic or adventitious roots from the stem are present in the embryo, so that the seminal root system may consist of a main tap root and several laterals. When the primary root continues to develop and forms a conspicuous structure from which numerous laterals diverge, it is referred to as a *tap root* whether slender or fleshy. If the primary root and its laterals develop more or less in equal degree and are relatively numerous, the root system is *fibrous*. In some cases, the primary root system persists only for a relatively short time, and the permanent roots arise adventitiously in a succession of whorls from the lower nodes of the stem.

Intergrades exist between the several types, and it is not uncommon for a plant to develop a deeply penetrating tap root together with a mass of fibrous surface laterals. Differences in soil texture and water content, and variations in methods of cultivation often affect to a very considerable degree the general configuration and

development of roots. Weaver (13) and Weaver and Bruner (14) have described and discussed the roots of the principal field and vegetable crops in connection with these points.

GROSS MORPHOLOGY. — The root axis differs in certain anatomical respects from that of the stem so that generally it can be distinguished from the latter on the basis of its structure. A representative root in which the differentiation of primary tissues is complete has three well-defined regions, *epidermis*, *cortex*, and *stele*. The epidermis consists of a single layer of thin-walled cells which are devoid of cuticle and have the potentialities to form root hairs by a lateral extension of their outer walls. The number and character of development of root hairs depend upon the species involved and the soil conditions. Centrad to the epidermis is the cortical region, consisting of several layers of parenchymatous cells that are limited internally by a uniseriate endodermis which is regarded as a part of the cortex. The endodermal cells have Casparyan thickenings that are usually more clearly defined than those of the endodermis of most stems. At maturity, the inner tangential, radial, and end walls of some of the endodermal cells may be appreciably thickened; while others, which lie approximately outside the protoxylem points, may have their walls thickened to a lesser degree.

The primary root of dicotyledons typically has a *radial protosteple*; or, less frequently, a *radial siphonostele*. The former consists of a central mass of primary xylem tissue with two to several radiating arms extending centrifugally to the pericycle. The latter constitutes the outermost layer of the stele, and lies immediately adjacent to the endodermis. At the time of maturation of the primary tissues of the stele, the pericycle is commonly a single layer of cells which form a continuous cylinder; but, in some instances, it may be interrupted by the protoxylem cells which directly abut the endodermis. In some roots, the pericyclic cells become active and undergo division prior to the complete maturation of the vascular tissues, and this frequently happens where there is an early differentiation of lateral roots.

Between the radiating arms of xylem are located the two to several groups of primary phloem; and, between the xylem and phloem, there may be a zone of parenchymatous cells from which a cambium may be differentiated. The number of protoxylem strands is fairly constant for a given species, but some variation

may occur, and it is not uncommon for a plant to have a different number of points in the primary root as compared with its laterals. The most common types are the *diarch* (two protoxylem points), represented by the primary roots of Beta, Solanum, and Raphanus (Fig. 12.); the *triarch*, found in Pisum and Medicago (Fig. 13); and the *tetrach*, in Cucurbita, Gossypium, and Ipomoea. (Fig.

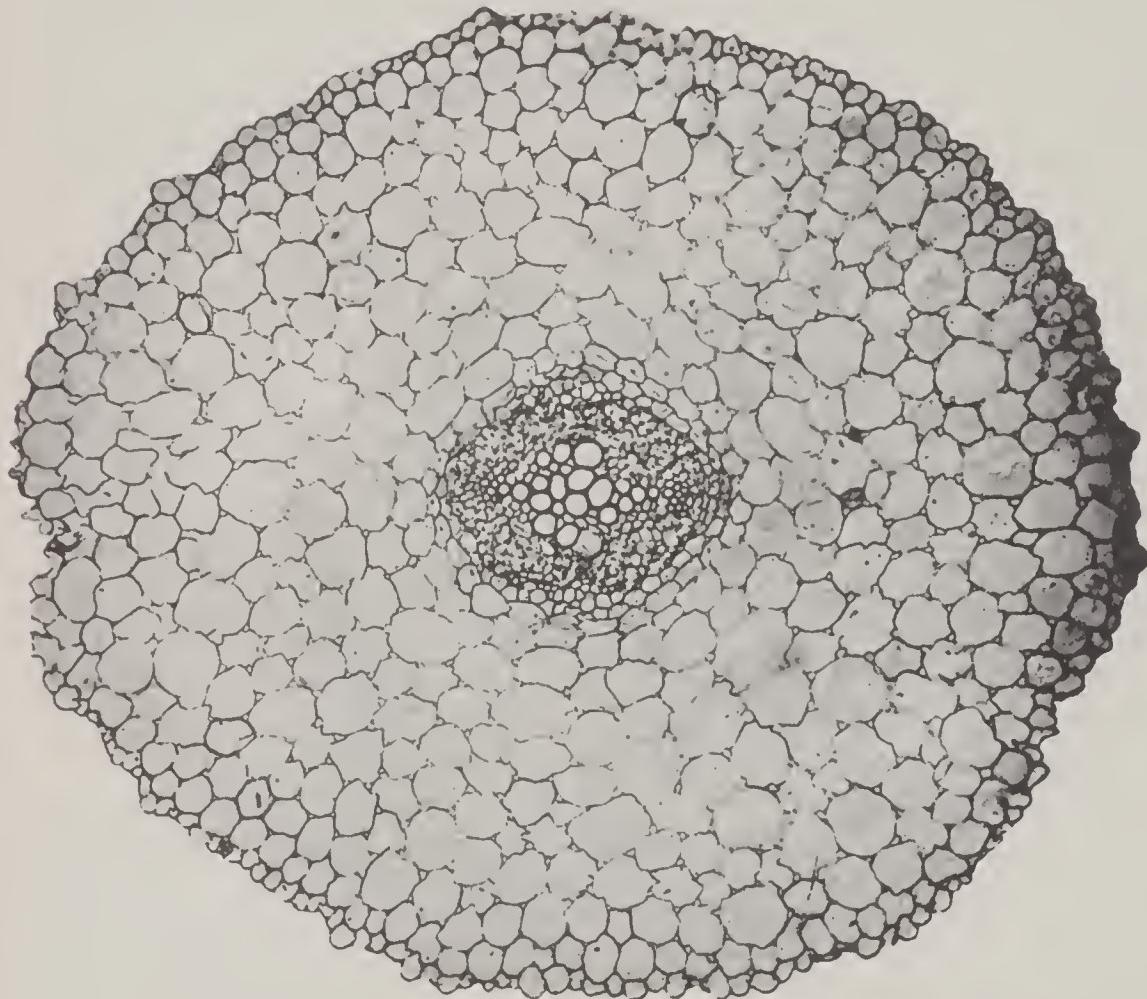


FIG. 12. Transection of the primary root of Raphanus showing the diarch primary xylem strand prior to secondary thickening of the axis. Outside the right-hand protoxylem point, the pericycle has divided tangentially, initiating lateral root formation.

310.) *Pentarch*, *hexarch*, *septarch*, and *octarch* types occur; and, in the Gramineae, there may be a larger number of arcs. In the radial siphonostele, the number of xylem arcs is usually considerably greater than found in radial protosteles; and they are commonly designated as being *polyarch*. (Fig. 14.) The number of arcs in the primary root of corn may be 20 or more; and, in secondary roots, twice that number frequently occur.

In some of the older literature dealing with the stelar anatomy of the root, the term *axile bundle* has been used to designate the pro-

tostele of the root, as well as the single vascular strand in the stem of certain hydrophytic dicotyledons; and the term *monostele* has also been applied as a synonym for protostele. The former term arose prior to the development of the stellar theory, and the latter has been largely superseded by the term *protostele*. In radial siphonosteles, the adjacent groups of xylem and phloem occurring on separate radii have been termed *radial bundles*. Inasmuch as the

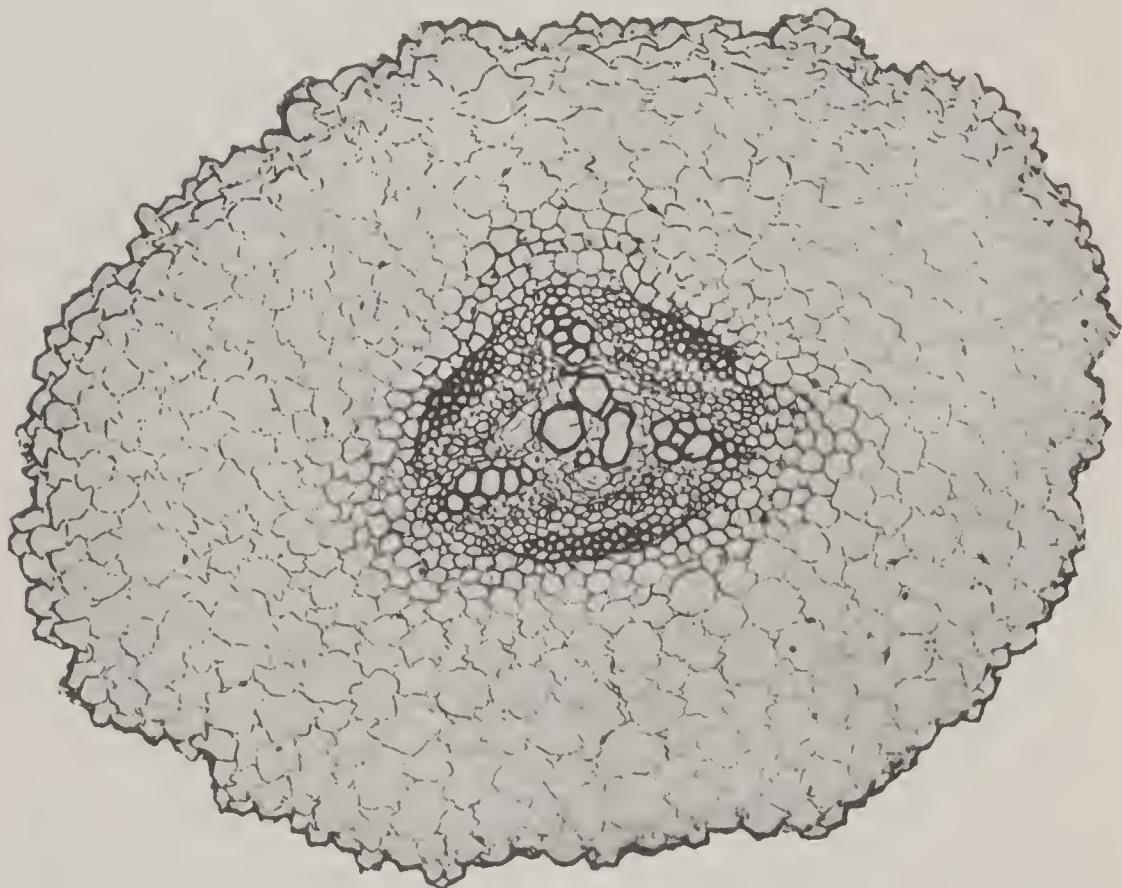


FIG. 13. Transection of the primary root of *Pisum* showing the triarch primary xylem strand and the development of phloem fibers adjacent to the pericycle. Outside the uppermost protoxylem point a pericyclic cell has divided tangentially, initiating lateral root formation.

primary xylem and phloem tissues are definitely separated by non-vascular tissue, it is probably more accurate to reserve the term *bundle* for those cases in which the two tissues arise from a single provascular strand and to designate the relation of the primary xylem and the phloem in the root as a radial arrangement.

ONTOGENY OF THE PRIMARY ROOT. — The primary root, or at least the apical growing point, is developed during the early stages of embryogeny. The degree of development attained prior to germination varies greatly, ranging from an undifferentiated zone of meristem terminating a short conical hypocotyl (*Cucurbita*), to

a well-organized root with a root cap and partially differentiated stele (*Zea* and *Lactuca*). Even in the former instance, in the very early stages of germination, the peripheral cells of the meristem divide rapidly; and, before the emergence of the root tip from the seed coat, a root cap (calyptra) is organized.

The root cap persists throughout the life of the root. As growth and development proceed, it is reduced outwardly by the abrasion and disintegration of the outer cells as the root penetrates the soil, and is renewed from within by the addition of new cells from the meristem. Thus, it maintains a relatively uniform size. In a

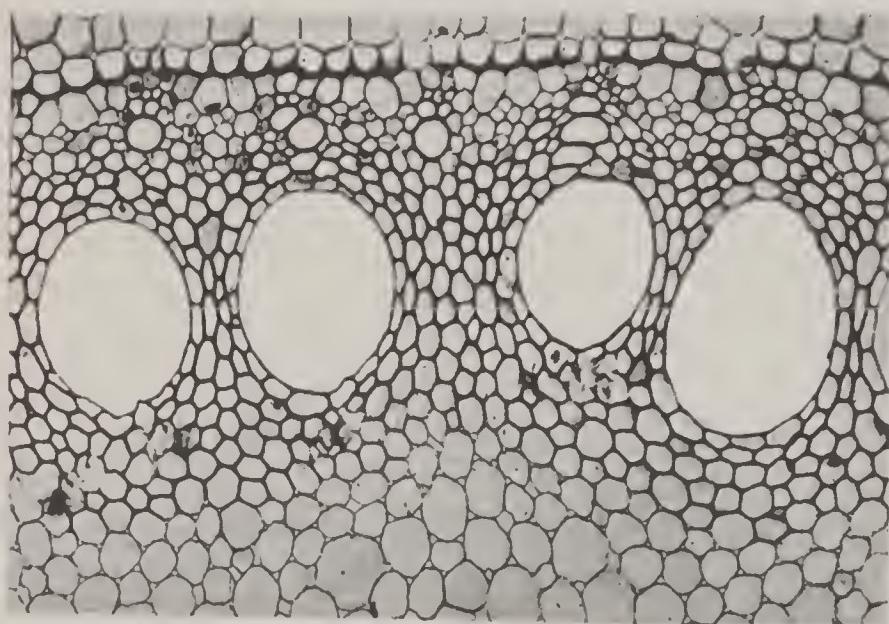


FIG. 14. A sector of the polyarch stele of the corn root showing the thick-walled endodermis with passage cells, the pericycle, protoxylem points with thin-walled phloem elements lying on alternate radii to them, the large metaxylem vessels surrounded by thick-walled connective tissue, and the pith.

median longisection of a root tip, it appears as a more or less conical cap several layers thick at its apex which decreases in thickness laterally.

After considerable growth and elongation, the primary root is divisible into several regions, in addition to the *root cap* and the *growing point* it surrounds. Directly back of the growing point is a zone known as the *region of elongation*, in which the newly formed cells are increasing in size, chiefly by the elongation of the component cells in the axial direction. This region is relatively short and merges insensibly into what may be termed the *zone of differentiation*, in which many of the cells may continue to enlarge and some still divide, but the majority begin to develop the special characteristics of the several tissues which constitute the primary

regions of the root axis. Further back is the *region of maturation*, in which the primary tissues attain the characteristics which they possess at maturity. The designation of regions of elongation, differentiation, maturation, and maturity in describing the ontogeny of the root axis is one largely of convenience, and there are of course no sharp boundaries delimiting these zones. There may be continued cell division in certain tissues of the developing axis, while the adjacent cells of some other tissue are compensating for this by cellular enlargement. In addition, some cells, even in the mature region, retain meristematic potentialities which may or may not later be expressed.

THE HISTOGENS. — The primary meristem at the tip of the root, where cell division is going on most actively, may itself be differentiated into regions. These are known as *histogens*; and, in ontogeny, the cells derived directly from them can be specifically related to the mature regions of the root. Hanstein (5) designated three of these regions as the *dermatogen*, *periblem*, and *plerome*; and, later, Janczewski (6) added a fourth, the *calyptrogen*. The latter term is applied when the root cap is derived from and maintained by the activity of a definite layer of meristematic cells distal to the other cells of the growing point. In cases where it is not possible to separate the meristematic cells that give rise to the root cap from others in the growing point, no specific designation is made except when the epidermis and root cap arise from a common layer. In this instance, the term *dermatogen-calyptrogen* has been applied.

The dermatogen, when distinct from the calyptrogen, consists of a single layer of cells underlying the latter, which perpetuates itself and produces epidermal cells by continued anticlinal divisions. The periblem is a generative layer inside the dermatogen which gives rise to the tissues of the cortex. In most cases, this histogen is one layer in thickness at the apex of the root; and, like the other histogens, it maintains itself by anticlinal divisions. The lateral cells of the periblem divide periclinally, so that the zone becomes several layered; and, subsequently, divisions of the derivative cells in three planes result in the formation of the cortical parenchyma and endodermis. The innermost histogen or plerome produces the stelar elements many of which are elongated; and the derivative cells divide transversely less frequently than do those of the cortex. This difference in the mode of cell division in the two adjacent regions derived from the periblem and plerome results in

a blocking off of the cortex and stele on the basis of cell shape; and, in many cases, it is possible to delimit them very early in ontogeny.

The degree to which the meristem is specialized into the four histogens is variable. Janczewski (6) has recognized four principal types of such meristematic differentiation in angiosperms. In type (1), the meristem is definitely and sharply differentiated into

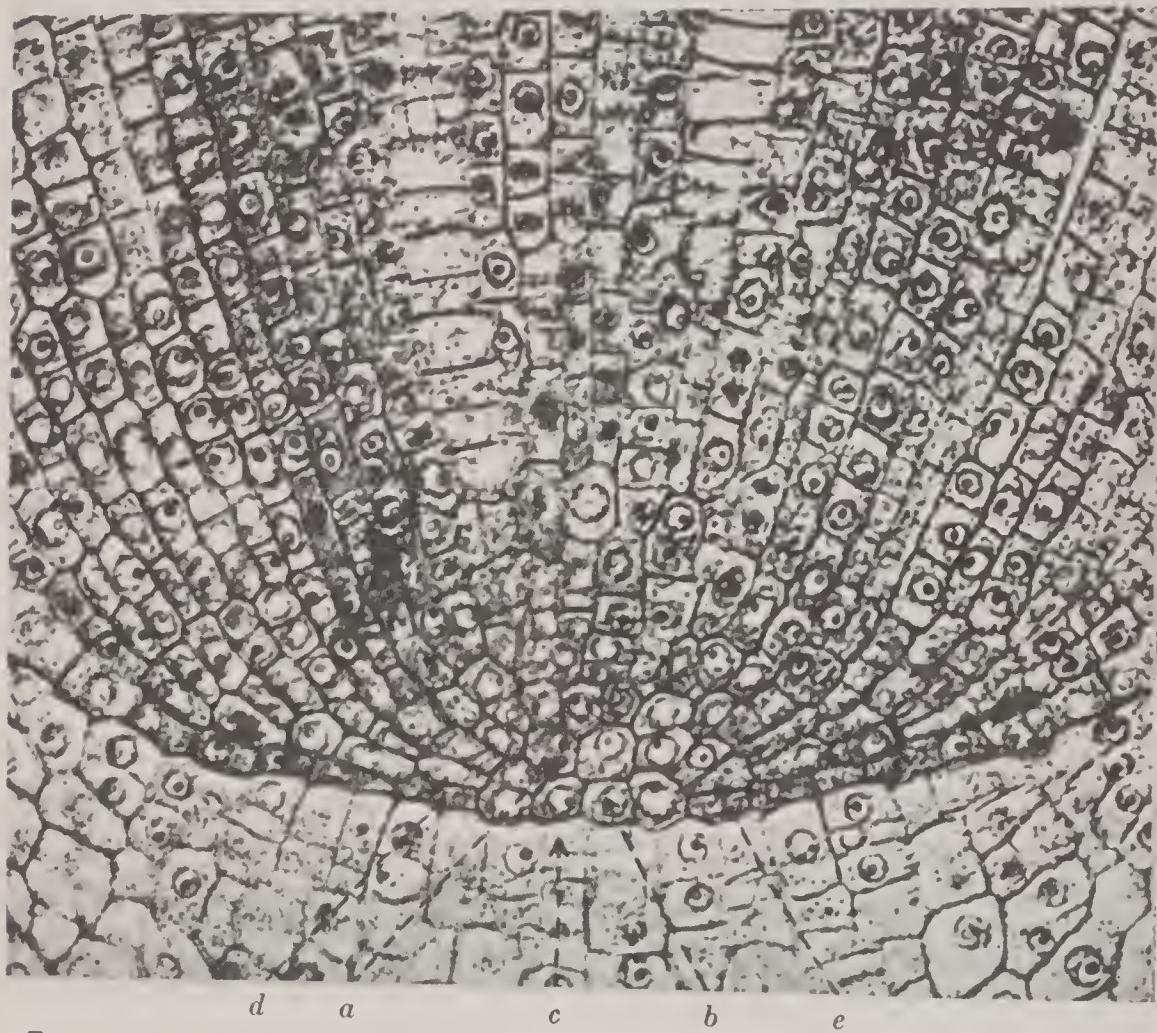


FIG. 15. Longisection of the apex of the corn root showing the histogens: *a*, the plerome; *b*, periblem which gives rise by periclinal divisions to the epidermis, *d*, and the cortical cells, *e*; *c*, the calyptrogen which produces the root cap.

the four histogens, plerome, periblem, dermatogen, and calyptrogen, from whose respective derivative cells the stele, cortex, epidermis, and root cap are developed. This type is an exceptional one, and does not occur in any of the economic plants later described. It is reported for a few hydrophytic monocotyledons in the family Hydrocharitaceae (*Pistia* and *Hydrocharis*).

At the apex of the root in type (2), the plerome and calyptrogen are sharply defined, and there is an intermediate layer between them

which is one cell layer in thickness. The lateral members of this intermediate zone divide periclinally, and the derivatives of the inner cells function as a periblem producing the cortical tissue, while the outer daughter cells become the dermatogen and form the epidermis. This is the type found in many monocotyledons including *Zea* and *Triticum*. (Fig. 15.) Treub (12) has described a modification of type (2) that applies to monocotyledons in which

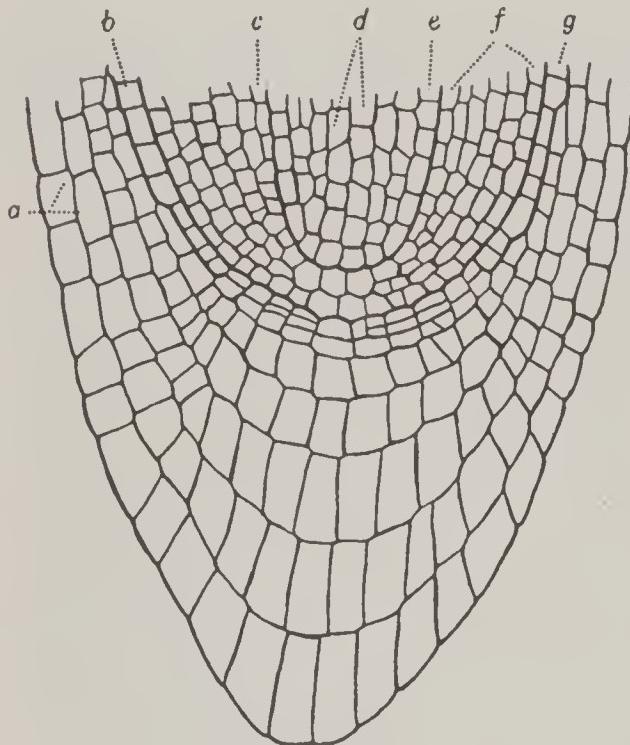


FIG. 16. Longisection of the apex of the root of *Linum* showing the character of the terminal meristem: *a* and *b*, root cap and epidermis respectively, derived from the calyptrogen-dermatogen layer; *c*, endodermis; *d*, stele, derived from the plerome; *e*, pericycle limiting the stele; *f*, cortex, derived from the two-layered periblem; *g*, epidermis. (After Janczewski, *Ann. Sci. Nat.*)

a definite calyptrogen is not differentiated. In this case, the root cap, epidermis, and cortex arise from a common group of initials two cell layers in thickness, and within this zone is a sharply defined plerome. In this modified type (2) are members of the Liliaceae, including the genus *Allium*.

In type (3), the plerome and periblem are sharply defined; and outside the latter is a common initial layer which produces the root cap and epidermis. The cells of this layer perpetuate the histogen by anticlinal divisions, and periclinal divisions at its apex form successive layers of the root cap, the innermost cells always functioning as the common ini-

itial layer. The cells of the common layer, which form the proximal margin, undergo a final periclinal division; and the inner daughter cells function as a dermatogen producing the epidermis by anticlinal divisions, while the outer ones are added to the root cap. Thus, according to Janczewski (6), the dermatogen and root cap are derived from the calyptrogen layer; but Crooks (3) and others, recognizing the dual character of the histogen, have designated it as the *dermatogen-calyptrogen* layer. In most cases reported as representing this type, the

periblem at the root apex consists of an initial cell or a single layer of a few cells which later becomes several layered by periclinal divisions. A variation occurs in *Linum* in which the periblem consists of two layers of cells overlying the plerome. The outermost layer divides only anticlinally to form the outer layer of the cortex or *hypodermis*, and the inner layer divides in all planes to form the remainder of the cortex. Type (3) is probably the most common one in dicotyledons; and occurs, among others, in *Raphanus*, *Ipomoea*, *Lactuca*, and *Linum*. (Fig. 16.)

In type (4) there is a common meristematic zone which extends across the apex of the root, and sharply delimited histogens are lacking. The peripheral cells of this terminal meristem enlarge and mature as the root cap. The stele and cortex arise from derivatives of the centrally located cells, and the epidermis is differentiated from the laterally placed ones.

This type is frequently referred to as the open type meristem. The Cucurbitaceae (*Cucurbita*)

and Leguminosae (*Pisum*, *Phaseolus*, and *Medicago*) are representative of this type. (Fig. 17.)

Irrespective of the type of meristematic organization, growth and differentiation occur in varying degrees; and there is an early blocking out of the epidermal, cortical, and stelar regions. In ontogeny, the cells of each primary tissue soon reach maturity, and the stelar pattern is laid down conforming to one of the protostelic or siphonostelic types noted above.

The dynamic aspect of root development is clear when successive transections of a root are studied through the regions of elongation

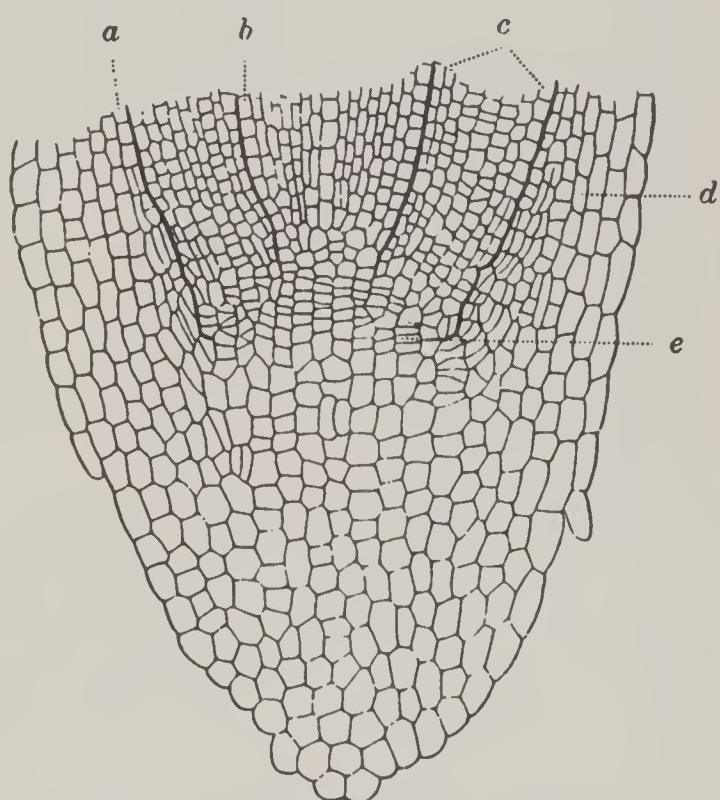


FIG. 17. Longisection of the apex of the root of *Pisum* showing the character of the terminal meristem: *a*, epidermis; *b*, pericycle limiting the stele; *c*, cortex; *d*, root cap; *e*, meristem. (After Janczewski, *Ann. Sci. Nat.*)

and maturation and up to the point where the primary tissues are mature. On the basis of such an examination, it is evident that the differentiation and maturation of the several types of cells do not proceed with equal rapidity. Various stages of differentiation of the xylem may be observed at a given level owing to the fact that the development of the primary xylem is a progressive process in which the protoxylem elements are the first to mature, followed later by those of the metaxylem. Similarly, there is a progressive differentiation and maturation of the primary phloem; and the appearance of well-defined sieve tubes and companion cells follows the initial differentiation of slender parenchymatous protophloem elements. Like the stelar elements, the endodermal tissue undergoes a succession of stages leading to maturation, passing through primary, secondary, and tertiary phases of wall thickening as described in the preceding chapter. The degree of epidermal differentiation may be gauged by the origin of the root hairs, which reach a maximum production in the region of maturation. Many subsequently die and disintegrate as the root hair zone is extended or additional ones develop.

SECONDARY THICKENING. — In many roots, especially those which are fleshy, increase in the diameter of the axis is accomplished by secondary thickening. This is usually initiated upon the completion of the maturation of the primary stelar tissues, but may begin before this process is entirely completed. The first stages of secondary thickening occur in the zone of fundamental parenchyma which lies between the primary xylem and phloem strands. At points centrad to the primary phloem strands, the parenchymatous cells begin to function as a cambium and divide tangentially and radially. The derived cells differentiate, maturing as secondary phloem elements centrifugally, and secondary xylem elements centripetally.

From the points of initial cambial activity, there is a progressive tangential development; and the zones of cambium are extended laterally until they reach the points where the protoxylem strands abut the pericycle. In this way, a continuous meristematic cylinder is formed, including the sectors of the pericycle from which the broad parenchymatous rays are derived. (Fig. 18.) The manner in which this occurs results in a rounding out of the xylem portion of the stele. The first secondary xylem elements derived from the cambium are laid down in the angles between the protoxylem

points, and the continued differentiation and maturation of secondary xylem ultimately smooths out the curve. In some cases, not all of the fundamental parenchyma lying between the primary xylem and phloem is involved in this cambial activity and there is a narrow zone of this tissue remaining between the primary and secondary xylem.

The elements which constitute the secondary tissues of the stele are derived from the cambium in such a way that at first they tend to lie in regular radial rows; but these may become somewhat irregular as growth and maturation proceed. This occurs in part because of the unequal growth rate of the elements, some of which attain larger size than others. In addition, the subsequent divisions and growth of some of the parenchymatous elements derived from the cambium may result in displacement and reorientation of the secondary tissues. (Fig. 19.) The secondary xylem consists of tracheids, vessels (tracheae), parenchyma, and fibers. The secondary phloem commonly includes sieve tubes, companion cells, parenchyma, and occasionally fibers and secretory tissue. The relative proportions of the constituent elements in the xylem and phloem, especially with reference to the parenchymatous cells, varies strikingly with the species of plant; and, where there is considerable secondary thickening, the amount of storage parenchyma may be large.

The continued enlargement of the stele results in definite changes in the outer portion of the axis. The primary phloem groups are forced outward, and this tissue is usually crushed or digested. The pericycle remains active and by radial divisions of its cells increases

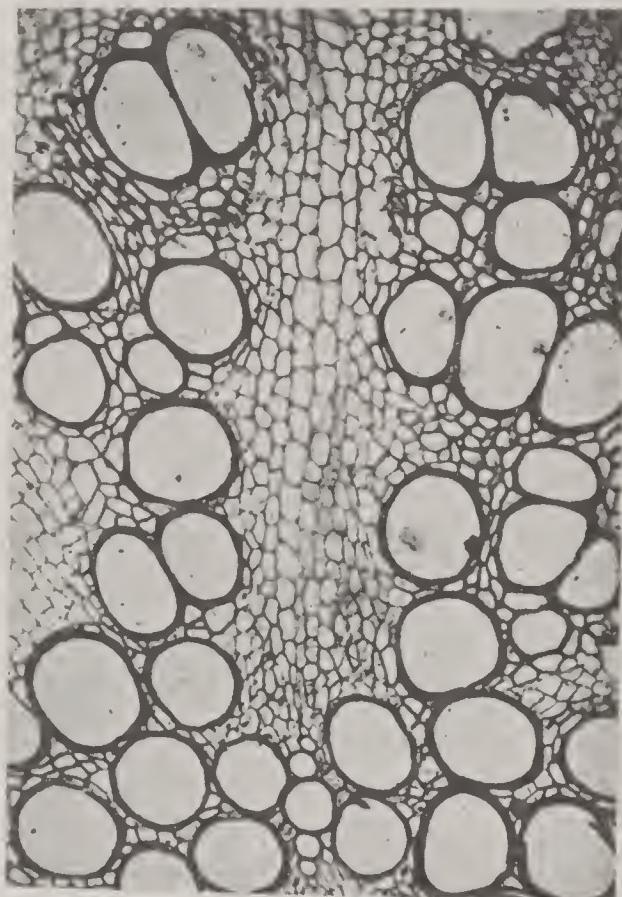


FIG. 18. Transection of a portion of the root of *Brassica* showing the diarch primary xylem strand, the broad pericyclic ray, and the secondary xylem.

in circumference, so that it persists as a continuous zone outside of the secondary phloem. Commonly, the pericyclic region also increases in width, owing to successive tangential cell divisions;

and this results in the formation of a few to many-layered zone of active pericyclic tissue. The epidermis, cortical parenchyma, and endodermis become fractured and disintegrate. As this occurs, the outermost layers of derivatives of the pericycle form a phellogen (cork cambium) which develops a protective periderm.

In many fleshy roots the pericycle may form a zone of storage parenchyma; and, in some cases, the term *secondary cortex* has been applied to this region. Since it is clearly of stelar origin, this terminology is apt to be misleading; and it is more accurate and convenient to use the term *pericyclic zone*. In very old, woody roots, especially of perennial plants, the pericycle may also be lost; and, when this occurs, a new protective periderm is formed from a phellogen

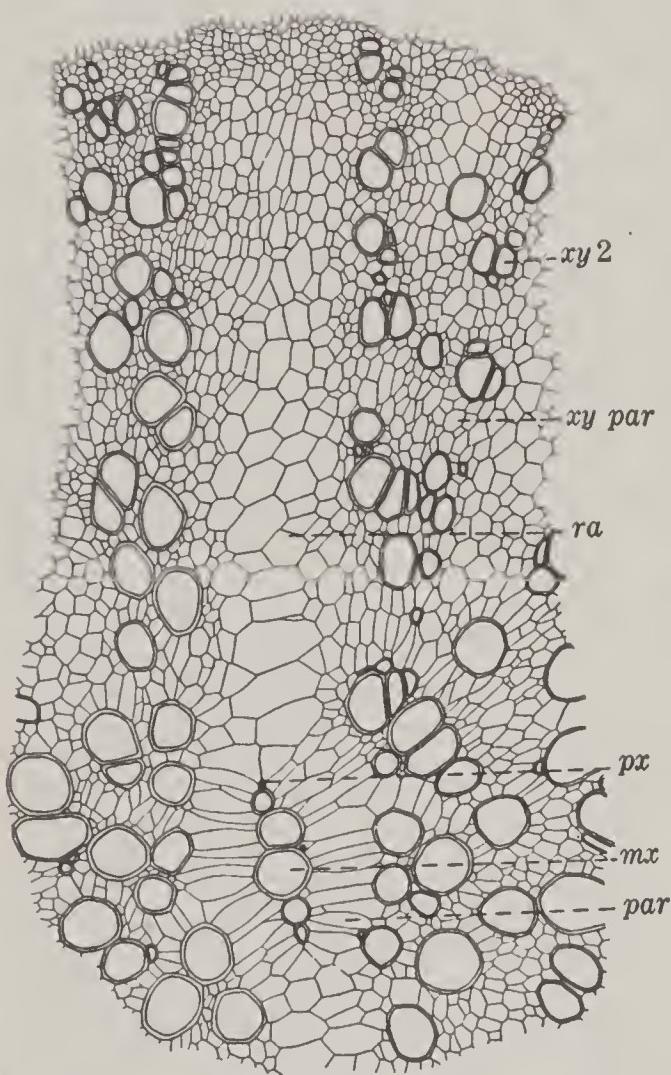


FIG. 19. Transection of a sector of the stelar portion of an old root of *Pastinaca* showing the primary xylem strand and the development of secondary xylem. The enlargement and division of the parenchymatous cells have resulted in a dispersion of the secondary xylem vessels: *mx*, metaxylem; *par*, interstitial parenchyma which has become radially elongated; *px*, protoxylem; *ra*, pericyclic ray; *xy par*, xylem parenchyma; *xy 2*, secondary xylem.

arising in the tissues of the secondary phloem and other tissues outside the cambium may be lost, the primary xylem remains in place at the center of the axis. Frequently, there is a proliferation of the cells of fundamental parenchyma adjacent to the primary xylem strand, or separating the metaxylem from the protoxylem, and this results in a spreading

and dispersion of the primary xylem elements so that the original configuration of the protostele does not persist in the mature root (*Pastinaca*). (Fig. 19.)

In addition to the usual methods of secondary thickening outlined above, certain anomalous cases occur in which the process is modified by the supplementary activity of both primary and secondary tissues. Among economic plants, this occurs in *Beta* and *Ipomoea*. In the former, further thickening is accomplished by the differentiation of secondary cambiums. These arise in rapid succession in the pericycle and phloem parenchyma, producing a series of concentric rings of vascular and parenchymatous tissue which lie outside the secondary xylem and phloem tissues formed by the primary cambium. (Chap. IX.) In *Ipomoea*, secondary thickening involves the formation of secondary cambiums which surround the protoxylem points. These may develop throughout the central portion of the axis, forming numerous zones adjacent to the secondary xylem elements or even occasionally in the secondary phloem. (Chap. XVI.)

LATERAL ROOT FORMATION. — In angiosperms, lateral roots usually arise in the pericyclic tissue at loci directly outside the protoxylem points although there are exceptions to this generalization. They are differentiated early in the ontogeny of the axis, usually prior to the initiation of secondary thickening. The first evidence of lateral root formation consists in the radial enlargement of two to several pericyclic cells adjacent to a protoxylem point. This is followed by tangential and radial divisions of the lateral root initials, and a conical growing point is formed. As a result of further growth, the lateral root primordium enlarges and elongates, forcing the endodermis and overlying cortical tissues forward so that eventually they are ruptured or laterally displaced.

In some roots, as in many cucurbits, legumes, and flax, the endodermal cells adjacent to the active pericyclic cells also enter into the early stages of lateral root formation, and may contribute to the formation of the peripheral cells of the newly formed growing point. In flax, the endodermis forms a single layer of meristematic cells overlying the root cap, and this remains active until the lateral root has pushed through the cortex of the primary root. In such cases, the pericyclic region differentiates the stelar portion of the lateral axis, and the endodermis and adjacent cortical cells of the primary root form the outer zones of the root primordium. A

slightly different situation occurs in *Zea* and other monocotyledons, in which the entire lateral root is formed from derivatives of the pericycle, except that the endodermis constitutes an exterior layer over the root cap.

In the organization of the growing point, the histogens are differentiated in the same manner as described for the primary root, and the type of ontogeny is similar to that of the axis from which the lateral root arises, although the number of points of protoxylem differentiated is not necessarily the same. The elongation of the lateral root primordium proceeds with varying degrees of rapidity,

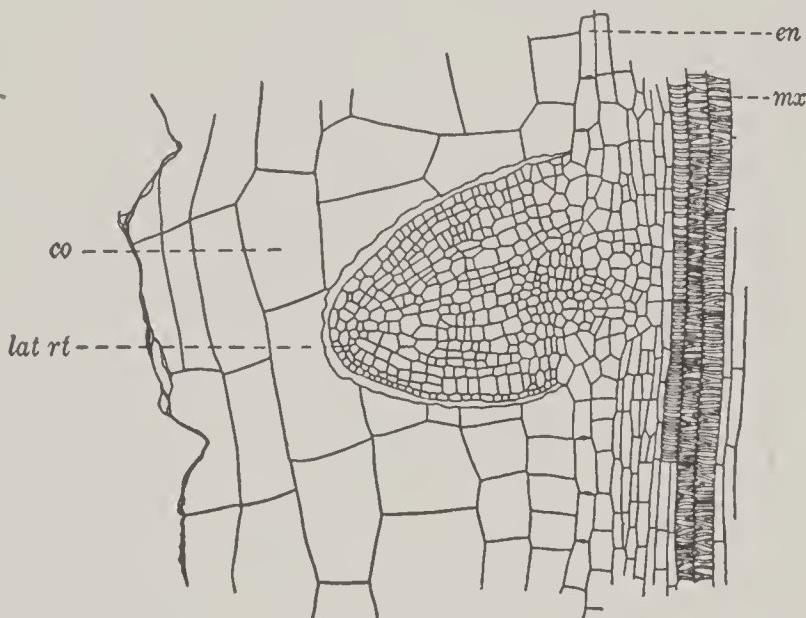


FIG. 20. Longisection of the primary root of *Pastinaca* showing the origin of a lateral root: *co*, cortex; *en*, endodermis; *lat rt*, lateral root; *mx*, metaxylem.

depending upon the plant and the environmental conditions affecting it; but, eventually, the cells of the endodermis, cortex, and epidermis of the main axis are either mechanically pushed aside and crushed, or are resorbed by the adjacent tissues. The point of origin of the lateral root is such that the cells of its stele are differentiated directly in contact with the vascular elements of the main axis; and, thus, the xylem and phloem of the lateral root may be continuous with the corresponding tissues of the main axis, but this is not true of the cortex and epidermis. (Fig. 20.)

In cases where secondary thickening of both the lateral and primary axes occurs, the cambium of the primary root and that of the lateral root may be continuous. As a result, successive additions of secondary vascular tissue to the two axes proceed simultaneously, and continuity of the vascular regions is maintained.

Because of the definite manner in which the lateral roots originate with respect to the protoxylem points of the primary stele, the number of rows of lateral roots is commonly equal to, or twice the number of, the protoxylem points, so that in a tetrarch root there are commonly four vertical rows of laterals, in a triarch root, three, etc. In diarch roots, the laterals are frequently initiated at a slight angle to the protoxylem point, and for this reason in roots such as *Apium*, *Solanum*, and *Lycopersicum* four rows of laterals arise. In many grasses, the lateral roots are initiated at points in the pericycle outside the primary phloem groups.

ADVENTITIOUS Roots. — In addition to the development of lateral roots from young root axes, they arise from other organs of the plant, especially the stem. Such roots are called *adventitious* or *adventive*. In the most restricted sense, the term is not ordinarily applied to roots arising from other roots, even though they are produced late in ontogeny and in the same manner as those which arise from the stem. The term is applied, in a broader sense, to all roots which do not arise from the pericycle and adjacent tissues in typical acropetal succession at about the time when secondary thickening of the axis has been initiated. On this basis, roots formed late in ontogeny from the peripheral tissues of woody or fleshy roots and those arising as a result of injury to a mature root axis are regarded as adventitious.

The organization of the root meristem and the ontogeny of the adventitious root are similar in all respects to that described for the lateral root; but the point of origin of such roots deserves further consideration. In general, the origin of adventitious structures, including both roots and shoots, requires the presence at the point of origin of potentially meristematic tissue. For this reason, adventitious roots frequently arise from intercalary meristems at the bases of internodes, from the meristematic tissue which commonly occurs at the axils of leaves, from lateral meristems such as the cambium and pericycle, from ray parenchyma; and, less frequently, from the parenchymatous tissue of other regions.

In the case of roots arising from stems, Priestley and Swingle (9) have noted that the tissue from which the root originates is determined in part by the age of the stem from which the adventitious root arises. In young stems, they are usually pericyclic in origin, arising from a group of cells rather than from a single cell.

Less frequently, they originate in phloem and ray parenchyma. The organization of the root meristem may involve several layers of procambial tissue in cases where the point of origin is not an internodal region, or in proximity to a node which is still in the meristematic condition and undergoing elongation. In older stems, the adventitious roots frequently arise in the parenchymatous ray tissue adjacent to the youngest secondary xylem and phloem elements; and the root primordium may be regarded as being derived from the ray or the interfascicular cambium. Some roots may arise from the persistent pericycle under these conditions; but the origin of roots from ray and secondary parenchyma derived from the cambium is more common.

Adventitious roots frequently occur at or near the nodal regions where the tissues are usually meristematic, at least in young stems; but the production of roots is not restricted to the nodal zone and they may develop at any point along the internode. This is illustrated in the production of adventitious roots in the first internode of *Zea*, and the formation of internodal roots in *Lycopersicum*. (Fig. 21.) A special case of adventitious root development occurs in some crucifers in which the origin of the root is exogenous instead of endogenous, involving epidermal and cortical tissues rather than stelar ones. This was demonstrated by Hansen (4) for *Cardamine*. In this case, the roots arise only in the axils of the leaves and are related to the axillary bud, forming a lateral out-growth from it.

Adventitious roots may also arise from leaves, but this is less common than their origin from stems. In the former, the root initials originate from parenchymatous tissues in close proximity to the cambium of the vascular bundles. This occurs in the leaves of *Begonia* and *Bryophyllum*. Crooks (3) demonstrated, in the excised cotyledons of *Linum*, that adventitious roots originate from a layer of parenchymatous cells on the adaxial side of the veins. LaRue (7, 8) observed the rooting of excised cotyledons of 41 plants belonging to 19 different families.

The whole problem of vegetative reproduction, including the production of adventitious roots, is associated with the retention of the meristematic capacity on the part of certain cells of the plant body. Where this occurs, the potentialities for further growth and differentiation of structures are limited only by the environmental conditions and the external and internal stimuli that may

be operative in any given case. The individual differences which exist in plants with respect to their capacity to respond to stimulus in the production of adventitious structures undoubtedly lie deeper than the matter of tissue relations, and may be hereditary.

The importance of the potentiality in economic plants to produce adventitious roots and shoots can hardly be overestimated.

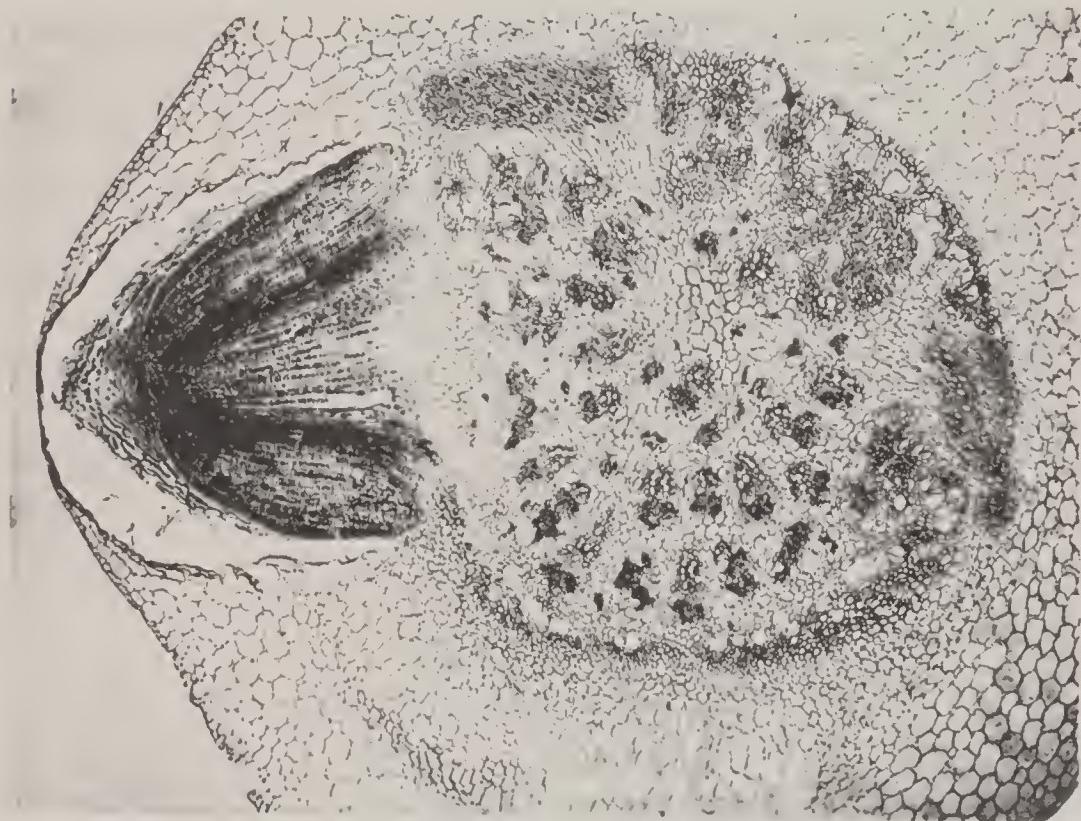


FIG. 21. The origin of an adventitious root in *Zea*.

Investigations by Robbins and coworkers (10, 11), Cooper (2), Zimmerman and Wilcoxon (15), Bonner (1), and many others of methods of artificial stimulation in the production of adventitious roots through the use of phytohormones and other growth-stimulating substances have been productive of most encouraging results.

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CHAPTER III

THE ANATOMY OF THE SHOOT

GENERAL MORPHOLOGY OF THE STEM

THE stem and its appendages, *foliage leaves* and *inflorescences*, constitute the *shoot*. The stem is typically an aerial structure; but, in some cases, it may be wholly or in part subterranean, producing underground branches some of which may be greatly specialized for storage.

In general form, the aerial stem may be erect and unbranched, bearing the leaves and flowers on a single vertical axis, or much branched with several axes of approximately equal size so that it develops a bushy crown. In a vine type, the stem may be prostrate as in *Ipomoea*, twining as in species of *Phaseolus*, or climbing by means of tendrils, *Pisum* and *Cucurbita*. In some plants, the stem does not elongate greatly during its early development, and forms a short conical crown of leaves. This type of growth may result in the formation of a bulb if the leaves are fleshy (*Allium*); a head (some species of *Brassica* and *Lactuca*), or a simple rosette (*Beta* and *Raphanus*). Later, the stem or a portion of it may elongate rapidly, forming an erect axis bearing foliage leaves and the inflorescence.

The principal types of underground stems are the *rhizome*, *tuber*, and *corm*. The rhizome consists of a more or less elongated underground stem which arises from a lateral bud near the base of the main stem axis and extends horizontally through the soil. Although it may have a superficial resemblance to a root, it has the anatomical characters of a stem with respect to the internal organization of its tissues. Externally, it may be recognized as such by its nodes and internodes, although the underground habit results in the reduction of the leaves diverged from it so that they are small and scale-like. Functionally, such stems are often storage organs, and a means of vegetative extension. Aerial shoots frequently develop from lateral buds of the rhizome, and adventitious

roots may also be produced abundantly. In *Solanum tuberosum*, the rhizomes extend outward in the soil for several inches and then the terminal portion begins to thicken, developing as a fleshy storage organ, the tuber. This, like the rhizome itself, is a true stem and has buds (eyes) in the axils of reduced leaves.

Closely related to the rhizome in general habit, and often confused with it, is the stolon or runner. Like the rhizome, this arises from a lateral bud near the base of the stem axis; but it remains on the surface of the ground rather than being subterranean. It develops adventitious roots and is a means of vegetative extension and propagation as illustrated in the case of certain stoloniferous grasses and the strawberry.

The corm is a type of underground stem in which the axis is short, vertical, and fleshy. There is a tuft of aerial leaves above, and a mass of fibrous adventitious roots below the stem, which is generally sheathed by the leaf bases. Typical examples of this structure occur in *Gladiolus* and in many of the *Orchidaceae*.

ANATOMY OF THE STEM

The stem differs from the root externally in the divergence from it of lateral members, the leaves, at more or less regular intervals. The places of such divergence are *nodes*; the intervals between them, the *internodes*. Histologically, it is composed of tissues similar to those in the root, the chief differences being the manner of distribution of the vascular tissue and the character and specialization of the epidermal layer.

THE HERBACEOUS DICOTYLEDONOUS STEM. — In most herbaceous dicotyledonous stems the vascular system constitutes a *dictyostele*, or *dissected siphonostele*. In such a stelar type, the vascular bundles which comprise it occur as a number of distinct longitudinal strands, so that in transection there is a ring of vascular bundles that are separated from one another radially by rays or zones of parenchymatous tissue. (Fig. 22.) Great variation exists with respect to the amount of parenchymatous tissue in proportion to the vascular tissues, either as cortex, pith, or rays. In some cases, even the vascular regions possess large quantities of parenchyma. The fact that parenchymatous tissues may be present in such very large proportions is one of the principal characteristics which may render a plant of economic value as food for animals and man. This is true because, in such tissues, large quantities of foods may be

stored for shorter or longer periods, and because these tissues are comparatively easily crushed or broken and the foods they contain readily released.

The primary bundles of the stem are typically *common bundles*. This term was first applied by Hanstein as referring to those bundles that are common to both stem and leaf, in contrast to *cauline bundles*, which originate in the stem and have no direct connection with the leaves. The common bundle originates at or near the base of the leaf primordium, and one extension of it forms a vein of

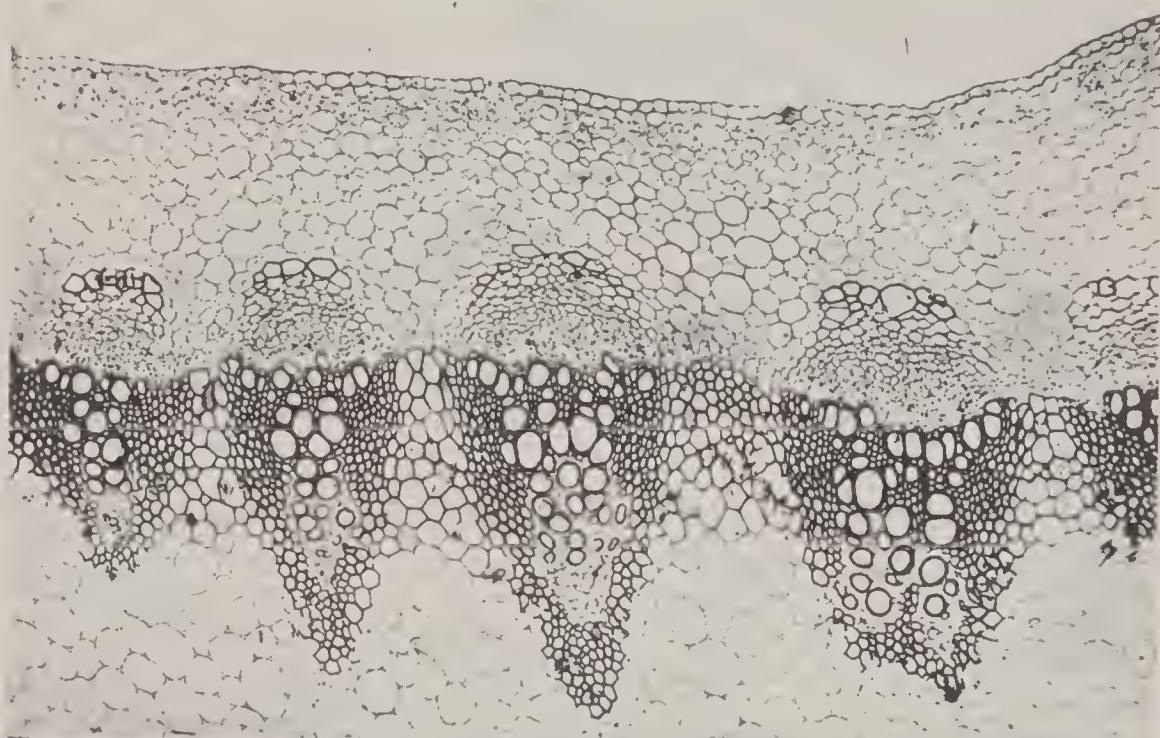


FIG. 22. Transection of a sector of a stem of *Raphanus* showing the vascular cylinder with the bundles forming a dictyostele. The phloem is subtended by groups of pericyclic fibers and the xylem is surrounded by thick-walled connective tissue. The ray parenchyma has also become thick-walled and there is a limited development of interfascicular cambium.

the leaf while the other follows an approximately perpendicular course down the stem axis. After traversing one or more internodes, it usually anastomoses with the common bundles of lower leaves. Cauline bundles may be cross-connected with common bundles by branches or by the development of secondary vascular tissue.

The bundles which comprise the dictyostele are usually *collateral*, although *bicollateral* bundles are not uncommon in certain plant families. (Fig. 23.) In the collateral bundle, the xylem and phloem lie on the same radius with the phloem external to the

xylem. In the b collateral type, the bundle is organized like the collateral one; but it develops an inner phloem as well as an outer one so that the xylem lies between two primary phloem groups. This type occurs in the Cucurbitaceae, Solanaceae, and Convolvulaceae; but there is some difference of opinion as to the interpretation of the bundle in certain members of the last two families.

The pericycle which lies outside the outer phloem is a continuous zone of cells one to several layers in width. In some instances, it can be clearly distinguished from adjacent tissues because of the differentiation of a complete ring of pericyclic fibers; but, in other stems, the fibers may be formed only over the phloem portion of the bundles where they serve as protective caps. The intervening

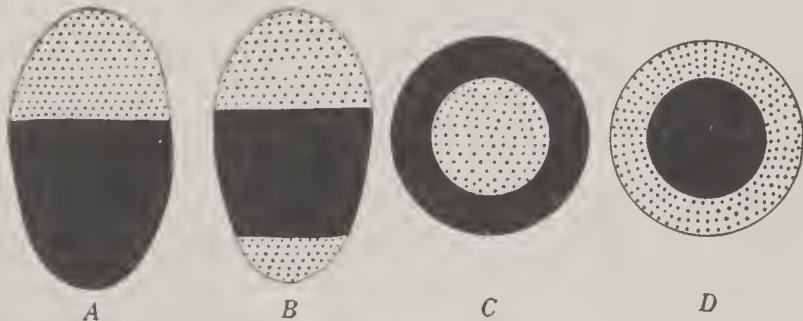


FIG. 23. Types of vascular bundles: *A*, collateral; *B*, b collateral; *C*, amphivasal; *D*, amphicribral. The stippled areas represent phloem, the black ones, xylem.

sectors of the pericycle may remain parenchymatous so that they cannot be separated on any histological basis from ray tissue; or, late in ontogeny, they may mature as stone cells. Because of the relationship of the pericyclic fibers to the vascular elements in many plants, the term *fibro-vascular bundle* has been employed; but, since fibers are not a constant feature of the vascular unit and in many cases often occur as distinct and isolated strands, the term *vascular bundle* is more commonly used.

Except in some underground stems and those of certain woody plants, the endodermis is generally not as clearly defined as it is in roots, since it often lacks characteristic Caspary strips. It may be distinguished in some cases by the size and regularity of its component cells, which are oval or rectangular in transection, by the presence of starch and other substances in the lumen of the cells, or by its characteristic physiological reactions. The cortical region consists mainly of thin-walled parenchymatous cells, the outermost layers sometimes containing chlorophyll. Frequently,

there is a peripheral zone of collenchyma which may form a continuous, several-layered cylinder immediately adjacent to the epidermis. In some cases it may be restricted to limited regions, as in angular stems where strands of collenchyma form reinforcing ridges and add greatly to the mechanical strength and pliability of the plant as a whole.

The epidermis constitutes the outer protective layer of the axis and is typically uniseriate. The cells of this tissue are compactly organized into a continuous layer which is uninterrupted except for stomatal openings. The outer and radial walls are usually

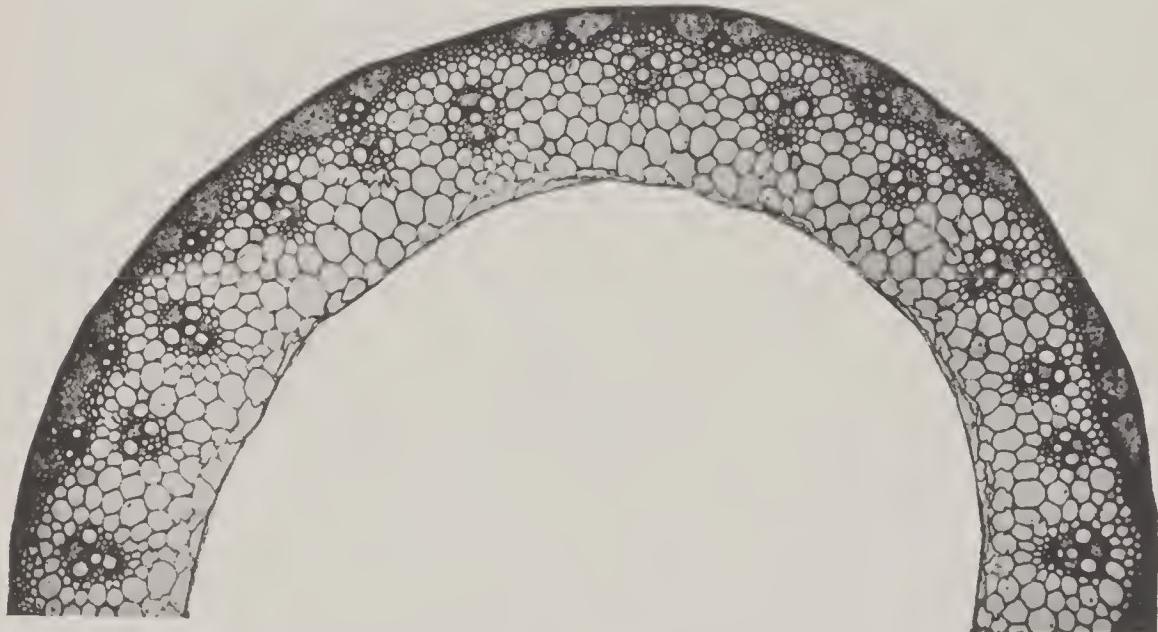


FIG. 24. Transection of a portion of a stem of *Triticum* showing the arrangement of the bundles, the distribution of the chlorenchyma and mechanical tissue, and the hollow center.

thicker than the inner ones, being cutinized or suberized; and they may be further water-proofed by the deposition of a non-cellular cuticle. Epidermal hairs, prickles, thorns, and other emergences may occur as noted in Chapter I.

THE HERBACEOUS MONOCOTYLEDONOUS STEM. — The stem of the herbaceous monocotyledon differs from that of the dicotyledon chiefly in respect to the components of the vascular bundles, which in most cases do not possess a cambium. The arrangement of the bundles may conform to the dictyostele type but meristyles are common. In *Triticum*, the stem bundles comprise a dictyostele with a central medullary region which may be hollow; while, in *Zea*, there is a meristele and the bundles are scattered through the fundamental parenchyma of the axis. (Figs. 24, 25.)

There is great diversity and complexity among monocotyledonous stems in regard to the course of the bundles of the meristele. In a large number of them, including the palms and some grasses, the bundles conform to the plan which is briefly summarized below. In these plants, the leaf base is very broad at its point of divergence and commonly encloses the greater part of the stem or completely encircles it at the node. Each leaf has a very large number of bundles (it may exceed 200 in *Zea*), and these enter the stem at the node, extend downward through several successive internodes,

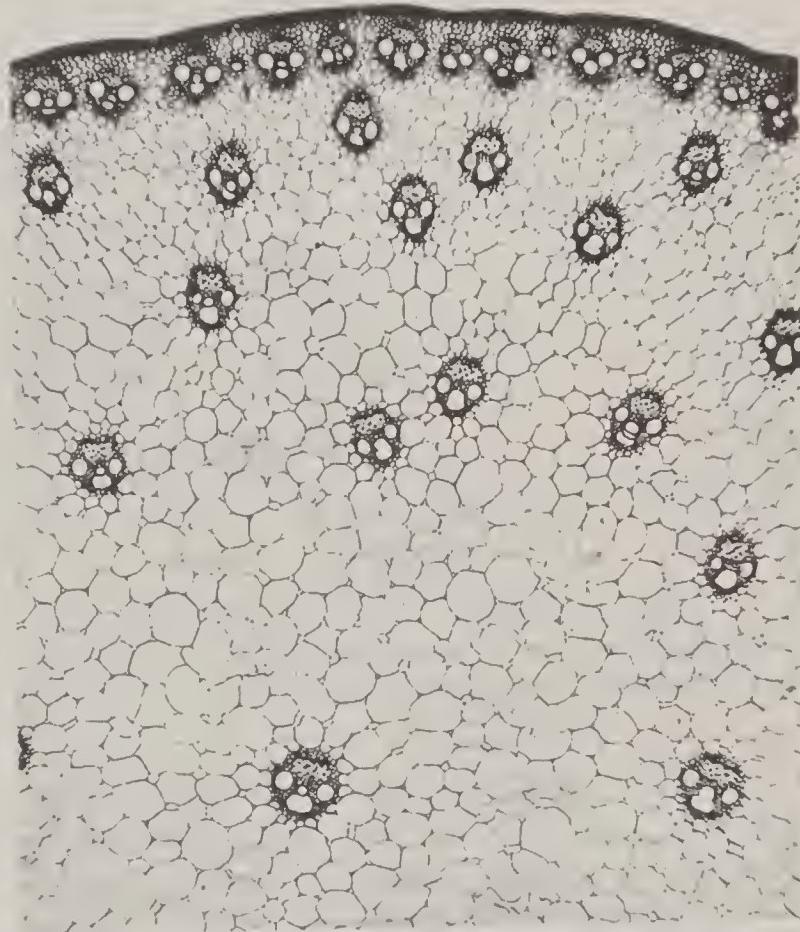


FIG. 25. Transection of a sector of a stem of *Zea* showing the distribution of the bundles and mechanical tissues.

and finally are united with the bundles of lower leaves. Because of the regularity with which the bundles are anastomosed with lower ones, and the uniformity of the distance that they extend down the axis, approximately the same number of bundles may be observed in transections at successive internodes.

Some of the bundles extend down the outer periphery of the vascular zone, while others lie nearer the center of the stem and

constitute the inner bundles of the meristele. The latter are usually the median or larger bundles of the leaves, while the smaller, marginal bundles are those which occupy the peripheral portion of the stele. The more crowded distribution of bundles in the outer zone of the vascular region is due to the fact that the bundles, except for the peripheral ones, do not describe a perpendicular course in the stem axis, but are differentiated in a radially oblique direction until they finally anastomose at lower levels with bundles of the outer zone. Since a single bundle may continue through several internodes before being united with another one, the effect of intercalary elongation of the axis is to straighten out the curvature, so that each bundle apparently describes a perpendicular course in the mature internode. The insertion and anastomosis of bundles with those lower in the axis occurs chiefly at the nodes, where a very complex nodal plate is formed consisting of a large number of transversely and otherwise oriented bundles.

The individual bundles which constitute the meristele vary in type. The most common is the collateral or half-amphivasal bundle, and less frequently a true amphivasal bundle is differentiated. A third type is the amphicribral bundle which commonly occurs in pteridophytes (*Polypodium*), but is rarely developed in angiosperms. In the collateral bundle of the meristele, the vascular tissues are usually oriented so that the xylem is centrad to the phloem; and, in amphivasal types, it more or less completely encircles the phloem with outwardly projecting arms of metaxylem, the development of the primary xylem being endarch. The mechanical tissue associated with the bundles consists of fibers or sclerotic cells which form a more or less complete ring around the bundle (*Zea* and *Triticum*). In addition to this mechanical tissue, the stem may have a zone of sclerenchyma immediately inside the epidermis, which is several layers in thickness and consists of small, compact, elongated elements.

ONTOGENY OF THE STEM Axis. — The apical meristem is protected from injury by the developing leaves and the bud scales when present. An unelongated axis of this kind with its leaves is called a *bud*, and its terminal portion consists of meristematic cells from which lateral members are differentiated exogenously. (Fig. 26.) The ontogeny of the stem axis is complicated by the manner in which these lateral members are initiated and differentiated, since the stelar organization of the stem depends upon the development

of the vascular bundles of the leaves and branches which in the aggregate constitute the stele.

The meristematic regions of the root and shoot are similar with respect to the characteristics of the cells which comprise them, but they differ markedly in other ways. One obvious difference is that the root meristem is surrounded and protected by cells differentiated from it which constitute the root cap, while the stem meristem is exposed except for the protection afforded by the leaves diverged

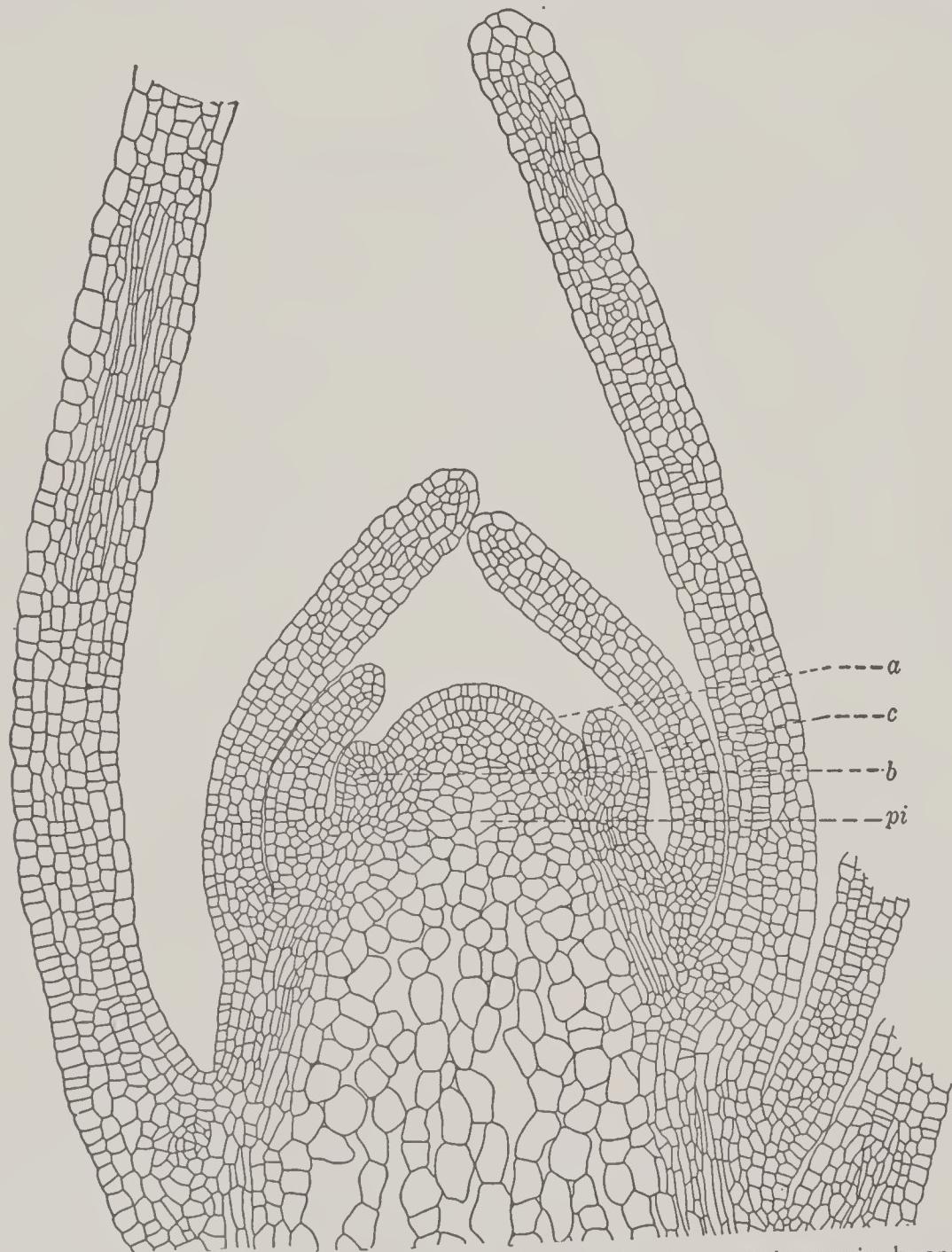


FIG. 26. Median longisection of the stem tip of *Linum* showing several stages in the ontogeny of the leaf: *a*, section of a very young leaf primordium; *b* and *c*, older primordia showing early development of provascular strands; *pi*, pith. (After Crooks.)

from it. Another fundamental difference exists in the manner of organization of the histogens and the way in which these respective layers undergo cell division. In the stem apex, the surface layer or dermatogen, as well as the one or two layers underlying it, divide anticlinally with the result that they increase in area without adding to the thickness of the axis. On the other hand, the more centrally located cells divide in all planes; but the rate of division is essentially the same in both cases, as demonstrated by Schüepp (35, 36). As Priestley and Swingle (30) have pointed out, the addition of cells to both the superficial and central regions at the same rate, coupled with the fact that the divisions of the dermatogen and adjacent layers are only anticlinal, while those of the inner layers occur in all planes, results in the formation of folds by the surface tissues, which become the initials of the new leaves. The further development of leaf primordia is discussed in a later section.

Deferring, for convenience in description, the discussion of the formation of the lateral members, the ontogeny of the stem axis may best be understood by considering the progressive development of the stem as represented at successive levels from its apex to a point where secondary thickening is initiated. At the apex, the meristematic growing point consists of thin-walled parenchymatous cells which are relatively small with a dense cytoplasm and prominent nuclei. These cells divide actively, and there is no evident differentiation among them except for changes in the shape of the cells of the outer layer (dermatogen) which, because of their position and internal pressure, may become tangentially elongated. It is in this region that the superficial folds occur which are the forerunners of leaf primordia.

Somewhat below this level, the differentiation of the provascular strands occurs. In herbaceous dicotyledons, these form a procambial cylinder in which the strands consist of groups of small cells that continue to divide while the adjacent ones increase in size and become more vacuolate. As progressive development occurs, the vascular cylinder becomes more sharply delimited owing to the increased growth and vacuolation of the parenchymatous tissue of the pith, cortex, and rays; and the appearance of larger intercellular spaces in these regions. The cells of the procambial strand continue to divide, and each strand may become somewhat extended tangentially as a result of such meristematic activity.

In longisections, these cells can be distinguished from adjacent parenchyma by their smaller caliber, greater length, and the density of their protoplasts.

At the level where the differentiation of the vascular elements begins, the endarch character of the xylem is indicated by the formation of protoxylem elements on the centrad faces of the pro-vascular strands. Simultaneously, or even slightly in advance of the development of the protoxylem, the first protophloem elements are differentiated on the outer face of the strand. The strands form common bundles which are direct continuations of those of the leaf. The point of their initial differentiation is at the level of divergence of the leaf primordium (at a node); and, from this point of initiation, the development of the bundle proceeds in two directions. Outwardly, it is continued into the developing leaf as a part of its vascular system; and, downwardly, it becomes a component part of the vascular system of the stem, where it ultimately is anastomosed with the vascular bundles of leaves diverged at a lower level.

At a level where the differentiation of the primary tissue is practically complete, the ring of vascular bundles is clearly delimited from the pith and cortex, and adjacent bundles are separated from one another by medullary rays. At this stage, the collateral bundle has an inner zone of endarch primary xylem, and an outer one of primary phloem. Between the two, a region of meristematic cells may remain undifferentiated, instead of maturing as primary vascular tissue; and this may function later as a fascicular cambium.

SECONDARY THICKENING OF THE STEM AXIS. — When the vascular bundle is collateral with an intervening zone of meristematic cells between the primary xylem and primary phloem, it is an *open* type. By continued activity, this meristem or cambium separating the primary vascular elements may give rise to cells which mature as secondary tissues.

In the formation of secondary vascular elements, the cambial cell divides tangentially to form two daughter cells. One of these remains meristematic while the other differentiates into either a secondary xylem or phloem element, either directly or after a subsequent division of the xylem or phloem mother cell. Such secondary division commonly occurs in the phloem where a new wall divides the mother cell into two unequal daughter cells, one of

which becomes the sieve tube, the other the companion cell. In general, a series of adjacent cambial cells divides simultaneously, and the daughter cells on one face differentiate into xylem or phloem respectively. The remaining daughter cells continue as cambial cells; and in this manner the cambium is perpetuated.

A further effect of the simultaneous division of adjacent cambial cells is that the elements formed from them lie in radial rows which may be very regular in their alignment. Variation in the subsequent development of the vascular elements, together with division of some of the derived cells, may disturb the radial symmetry of the secondary tissues, this being especially true in herbaceous stems. In addition to the tangential division of the cambial cells, divisions occur in other planes so that the cambium maintains itself as a continuous layer. Thus radial divisions take place which compensate for the increase in the circumference in the axis as secondary thickening proceeds. As Bailey (8) has pointed out, there are two general types of cambial activity which account for the increase in girth of the cambium. In pteridophytes, gymnosperms, and some of the dicotyledons that are less specialized structurally,

"the anticlinal divisions are more or less transverse and the products of these divisions elongate and crowd by one another, producing thereby an increase in the girth of the cambium and a non-stratified arrangement of its cells. In certain of the more highly differentiated dicotyledons, on the other hand, the anticlinal divisions are radio-longitudinal and the products of these divisions expand laterally, thereby increasing the circumference of the cambium, but they do not elongate to any considerable extent, and thus become symmetrically grouped in parallel, horizontal series."

The cambium initials are not all of the same size in a given plant, and Bailey (6, 7) has noted that the elongated fusiform initials may vary greatly in their nucleo-cytoplasmic ratio, while this is relatively constant in the smaller ray initials. The latter are much shorter than the fusiform initials whose derivatives mature as elongated vascular elements. With respect to the rhythm or sequence of formation of secondary xylem and phloem elements by the cambium, no specific statement can be made, except that the process is not necessarily a reciprocal one in which there is an alternate development of such elements. In general, the amount of secondary xylem produced exceeds the secondary phloem, which would mean that several successive layers of xylem mother cells

might originate from the cambium without the formation of a layer of phloem initials.

In secondary thickening, the dissected siphonostele may become a solid cylinder through the development in the ray tissue of an *interfascicular cambium* which is continuous with the fascicular cambium. This does not involve any movement or invasion of cells into the ray region, but is usually accomplished by a progressive activation of the parenchymatous cells immediately adjacent to the cambium in a zone which may be regarded as potentially procambial. This may proceed until there is a cambium completely across the rays. In other cases, the interfascicular cambium may occur first at a median point in the ray where a small bundle of secondary tissue is formed; and, later, by a lateral activation from this point, as well as from the fascicular cambium of the primary bundles, the cambial cylinder becomes complete.

There are varying degrees of development of interfascicular cambium, ranging from cases where none is formed and the vascular tissue remains as a dissected siphonostele at maturity, to those where the cambial cylinder becomes continuous and a solid zone of secondary vascular tissue is formed. The secondary tissues derived from the interfascicular cambium are not always vascular; and, especially in semi-herbaceous or semi-woody stems, the major portion of such tissue may consist of non-vascular *conjunctive* or *connective* tissue which by subsequent lignification affords added mechanical support.

In most monocotyledons, there is no secondary thickening, and enlargement of the axis is limited to the capacity of the primary cells to grow in size, although there may be a limited amount of division in the cells of the medullary and cortical parenchyma. In many instances, the tissue of the provascular strand is completely differentiated into primary xylem and phloem elements and no meristematic cells remain to form a fascicular cambium. This results in a bundle of the closed type. Arber (1, 2, 3, 4), Dauphiné (11), and Gatin (20) have reported intrafascicular cambium in monocotyledons, the first named reporting on 22 families in which some member has a cambium. There is no extensive development of secondary tissues, and the interpretation of the meristematic tissue of the bundle as a cambium in many of these cases is controversial. In some of the woody monocotyledons, such as *Yucca* and *Dracaena*, a type of anomalous secondary thickening occurs in

which the activation of pericyclic or cortical tissues, or both, results in the formation of secondary bundles and interfascicular parenchyma.

Secondary thickening is accompanied by changes in the cortical and epidermal tissues of the stem. When the development of secondary stelar tissue is not extensive, it may be compensated for by the growth and division of the cells of the outer regions of the axis; but where there is considerable secondary thickening, it usually involves a loss of the epidermis and often portions of the cortex. In such cases, a periderm is formed following the development of a phellogen which is initiated in the cortical or pericyclic parenchyma; or, infrequently, in the epidermis. The phellogen produces phellem (cork cells) centrifugally and phelloderm centripetally. (See Chapter I.)

Lenticels, which serve as aerating structures, are developed in the periderm when that tissue becomes extensive. They are commonly initiated at points beneath stomata, and the first step in their formation consists in the division of the cortical cells which form a group of loosely organized *complementary cells*. Later, the true phellogen arises and the growth of the peridermal layers causes an outbulging of the mass of complementary cells rupturing the epidermis at the stomatal opening. Continued activity of the phellogen at this point, or the production of successive phellogens, results in the formation of layers of complementary cells. More compact *closing layers* are also developed which serve to hold the spongy mass of complementary cells together. The closing layers are progressively ruptured by growth and stretching so that the margins of the lenticel appear irregular and fragmented. A typical lenticel is elliptical, somewhat raised above the surface of the bark, and is usually oriented with its greatest dimension in the vertical plane. They may become tangentially stretched where there is a persistent periderm as in *Prunus* and *Betula*.

VASCULAR TRANSITION. — In describing the ontogeny of the root and stem axes, no statement has been made with respect to the interconnection between the vascular systems of the two. The vascular organization is different in orientation and mode of development in the stem and root which together constitute the axis of the plant, and it follows that there must be a region of vascular transition at some point where continuity of the radial exarch protostele of the root with the endarch dictyostele of the

shoot is established. The transitional region may involve several internodes (three or four in *Pisum*), or it may be very short, occurring within a vertical distance of but a few millimeters in the hypocotyl (*Beta*). In the majority of cases, the transition is hypocotyledonary if the cotyledons are brought above ground in germination; but it may involve the first nodes and internodes above the cotyledonary node when the cotyledon or cotyledons are hypogean.

In the terminology of the seedling axis, the *hypocotyl*, where vascular transition most frequently occurs, is regarded as that portion of the axis immediately below the first node (cotyledonary node), in contrast with the *epicotyl*, which is the whole portion of the axis above that point. The two terms express axial relationships with respect to the first node of the plant from which the first leaves (cotyledons) are diverged; but they do not connote anything with respect to the structural organization of the portion of the seedling axis to which they are applied. Thus, the hypocotyl may be almost entirely root-like in structure, as in many hypogean forms (*Zea* and *Pisum*). On the other hand, the upper portion of a hypocotyl may be stem-like in structure as in many epigeal forms where the transition occurs in the lower and middle hypocotyl.

The manner in which the vascular transition is accomplished is constant for a given species, except for minor variations. It is brought about in ontogeny by a progressive reorientation of the vascular tissues which are differentiated in the embryo and by the apical and intercalary meristems of the hypocotyl. In a representative case, the vascular elements at the upper limits of the transition region are differentiated as endarch collateral bundles; and, at successively lower levels, the vascular strands are oriented in a radial relationship with an exarch development of the primary xylem.

While descriptions of specific vascular transitions tend to imply motion, the cells are laid down and differentiated in place so that the vascular reorientation is not accomplished by cell movement, but by a gradual change in the vascular pattern of the stele at each succeeding level of the transition region. In many cases, the changes involved are described as proceeding from the root and extending up the axis to the point where stem structure occurs, but this is done for reasons of convenience and clarity of description. In the actual ontogeny, the processes of growth and differentiation

proceed in the opposite direction, since the older portion of the axis is that part of the hypocotyl adjacent to the cotyledonary plate, and the tissues laid down distal to it are necessarily younger. Supplementary intercalary growth of the hypocotyl also may serve to complicate the description of transition in terms of progressive development.

The type of root-stem transition depends upon the character of the root axis, whether it is diarch, tetrarch, or polyarch; the character of the stem bundles, whether they are collateral or bicollateral; and the nature of the seedling development, hypogeal or epigeal. There are several well-recognized types of transition, and many of them are described in detail in connection with specific plants in later chapters. Regardless of type, the essential point of transition is that a reorientation of primary vascular tissues is effected so that vascular continuity may be established and maintained.

Sometimes actual continuity is attained only through the development of secondary vascular structures, but usually they are not involved. The cambial layer forms a lateral meristem which is continuous through root, hypocotyl, and stem; and the mechanism of secondary thickening is identical in all these regions. For this reason, the secondary vascular tissues are not only continuous throughout the axial extent of the plant, but have the same spatial relationships in the root, stem, and transition regions. There is no reorientation of the epidermis, cortical parenchyma, endodermis, and pericycle in the transition zone.

GENERAL MORPHOLOGY OF THE LEAF

The *shoot* has been defined as a stem axis with its divergent members, lateral branches, and leaves of various types. The principal leaf categories are: *foliage* leaves, which perform the photosynthetic function; *bracteal* leaves, which are primarily protective; *scale* leaves, or *cataphylls*, which may be vestigial or perform important functions in storage and nutrition; and *sporophylls*, which constitute the flower and are related to the function of gametic reproduction. Intergrades occur, a special case being that of the *cotyledons*, which may be related exclusively to the nutritive function, or may be nutritive in the early ontogeny of the seedling, and later carry on photosynthesis. Special leaf forms also occur, including *spines* and *tendrils*.

THE FOLIAGE LEAF. — The foliage leaf may be regarded morphologically as a lateral divergence from the axis, which, in the majority of cases, is expanded and dorsi-ventrally flattened. Its point of divergence is designated as a node, and usually one or several buds develop in the axil of the leaf, which may be vegetative or flower buds. In the former, the further development of the bud results in a branch bearing foliage leaves in the same manner as the primary axis from which it arises; while, in the latter, the bud develops as an inflorescence. (See Chapter IV.) In other instances, the bud may be dormant, developing later in the life of the plant; or, in the normal cycle of the plant, it may never develop further. Less frequently, there is apparently no bud in the axil; but it seems likely that the potentialities for bud development reside in the tissue at this point, and under some circumstances adventitious buds may be produced.

PHYLLOTAXY. — The leaf arrangement or *phyllotaxy* of the foliage leaves is often remarkably constant for a given species; and, consequently, constitutes a helpful diagnostic character. There are three principal phyllotaxies: *alternate*, in which a single leaf is diverged from each node (Fig. 27); *opposite*, in which two leaves are so diverged; and *whorled*, or *verticillate*, where there are three or more leaves at a node. In the alternate phyllotaxy, the leaves are arranged on the axis in a spiral; and because of the regularity of the angular divergence (the angle formed between two successive leaves) they are arranged in a definite number of ranks or rows. The relationship is commonly expressed fractionally. Thus, in the alternate arrangement, the $\frac{1}{2}$ divergence is the characteristic one for the Gramineae; the $\frac{1}{3}$ phyllotaxy is found commonly in the Cyperaceae, sedges; and the $\frac{2}{5}$ arrangement is perhaps the most common among dicotyledons. In this fractional expression of phyllotaxy, the denominator indicates the number of leaves or ranks in a complete cycle; and the numerator expresses the number of times the stem is encircled to complete a cycle. In a $\frac{2}{5}$ divergence, the cycle consists of five leaves and passes twice around the stem, so that there are five ranks or rows of leaves; and, starting at any given leaf, the sixth leaf lies in the same vertical plane as the first leaf. In the opposite arrangement, the successive pairs of leaves may lie in the same plane or at right angles to each other, and the latter type of phyllotaxy is often referred to as *decussate*.

Although the phyllotaxy of most plants is sufficiently constant

to indicate a genetic characteristic, variations often occur; and, in a single axis, two or more types may develop. In *Helianthus*, whorled, opposite, and alternate arrangements may develop on one stem; and similar combination phyllotaxies occur in *Linum*, *Cannabis*, and many other plants. Regardless of the system of phyllotaxy, there is an adjustment of leaves in relation to light so that the resultant leaf pattern or mosaic exposes a maximum amount of leaf surface to it.



FIG. 27. Types of phyllotaxy. *A, B, C*, various alternate arrangements; *D*, opposite arrangement. The upper figure in each case shows the phyllotaxy as seen from above. (From Smith et al., *Textbook of General Botany*.)

GROSS CHARACTERISTICS. — A representative vegetative leaf commonly consists of an expanded *blade* or *lamina* and a *stalk* or *petiole*. The latter is variable in length and in the sharpness with which it is delimited from the blade. Some leaves are non-petiolate and sessile. A special type occurs in the grass leaf, in which a basal *sheath* surrounds the axis; and, at its upper limit, there may be a *ligule* or collar-like membrane which clasps the stem.

In other cases, *stipules* develop which are generally regarded as divergences from the base of the leaf. Sinnott and Bailey (38) have

stated that the facts "favor the contention that stipules are integral portions of the base of the leaf, a view which is well expressed by Eichler when he says that stipules arise without exception as a product of the leaf-base of the primordial leaf." Recent work by Cross (10) on *Morus*, which attacks the problem from the stand-point of foliar ontogeny, confirms this point of view. In some instances, the stipules are very prominent as in *Pisum*, where they are large and perform the same functions as the blade. Some stipules are protective in relation to the axillary bud, others differentiate as spines.

The blade may be variously specialized; and differences in its color, shape, marginal characteristics and venation result in a great number of forms. Typically, the foliage leaf is green owing to the presence of chlorophyll in the mesophyll; but this pigment may be masked by the presence of accessory pigments, chiefly anthocyanins; and, in variegated leaves, the chlorophyll may be restricted to definite regions of the blade.

The shape of leaves may range from the slender, needle-like leaves of many conifers and the linear or lanceolate types found in grasses, to the more expanded ovate, cordate, or orbicular leaves which are commonly developed in dicotyledons. The degree of marginal modification varies from those which are smooth and entire through a progressive series of marginal indentations that include the serrate, dentate, and crenate forms. Where the cutting of the margin is more pronounced, the leaf is lobed; and this may be palmate (*Gossypium* and *Cucurbita*) or pinnate (*Raphanus*). If the blade is divided into segments or leaflets, the leaf is compound; and the arrangement of the leaflets may be palmate (*Cannabis*) or pinnate (*Pisum* and *Apium*).

The venation of the blade may be parallel or netted. In the former, the primary veins extend through the lamina parallel to one another without conspicuous anastomoses; while in the netted system the veins form a complicated reticulum. Studies of characteristic systems of parallel venation (*Zea* and *Allium*) indicate that there are many small cross-veins interconnecting the parallel members of the system. In the net-veined types, the ultimate veinlets commonly end blindly in a small area of chlorophyll parenchyma which is termed a vein islet.

The foliage leaf may persist throughout the life of the plant, or through several seasons in perennial plants. Evergreen leaves

occur on many conifers, and are also found on such trees as the olive, orange, and others. Many perennials have a deciduous habit, and a new set of foliage leaves is differentiated each year which is shed at the end of the growing season, or at the beginning of the ensuing period of vegetative extension. In annual plants, it is not uncommon for the cotyledons and basal leaves to be shed before the growth cycle is complete. In deciduous types, leaf fall is commonly accomplished by means of an *abscission layer*, which is usually located at the base of the petiole, but may sometimes be developed at the base of the lamina or at an intermediate point in the petiole. The separation of the leaf from the axis results from the development of the cells of the abscission layer which round off and separate from one another owing to the disintegration of the intercellular substance of their middle lamellae. A detailed account of this phenomenon is given for *Lycopersicum*. (See Chapter XVIII.)

ANATOMY OF THE LEAF

The leaf may include all the types of tissues which are differentiated in the stem (epidermis, parenchyma, mechanical, and vascular tissues). As might be expected on the basis of the ontogeny of the leaf, these tissues are continuous with those of the stem axis. Thus, the epidermis of the adaxial and abaxial surfaces of a foliage leaf forms an uninterrupted protective layer with the epidermis of the stem; the vascular bundles of the leaf are continuous with those of the stem axis at the node, and the parenchymatous regions of the petiole are contiguous with parenchyma of the stem.

Structurally, the leaf consists of three major regions: (1) the protective *epidermis*, which covers its entire surface, (2) the *mesophyll*, which is generally parenchymatous, and (3) the *veins*. (Fig. 28.) The character of the epidermis, the specialized stomatal apparatus, and the types of epidermal hairs which may be produced by this tissue have been discussed. (Chapter I.) The epidermis may be regarded as consisting in most cases of an impervious, non-chlorophyllose (except for the guard cells) layer which may or may not develop a non-cellular cuticle. Stomata occur in varying frequencies and distributions, so that ready means of gas exchange is provided. The number of stomata on the abaxial surface usually exceeds that on the adaxial one when leaves are oriented dorsiventrally. In those that assume a more or less vertical position

(many of the Gramineae), the stomatal frequency may be approximately the same for both surfaces. Stomatal counts are often at variance, owing to the fact that the number of stomata per unit area for a given species or even for a single plant may vary depending upon the age of the leaf and the environmental conditions under which it has developed. Expressed in approximate ratios, *Pisum* has about twice as many stomata on the abaxial surface as the adaxial one; in *Triticum*, the ratio of adaxial to abaxial stomata is about 10 to 7; and in *Zea*, 3 to 5. In *Olea*, olive, and *Ficus*, rubber plant, no stomata occur on the adaxial surface.

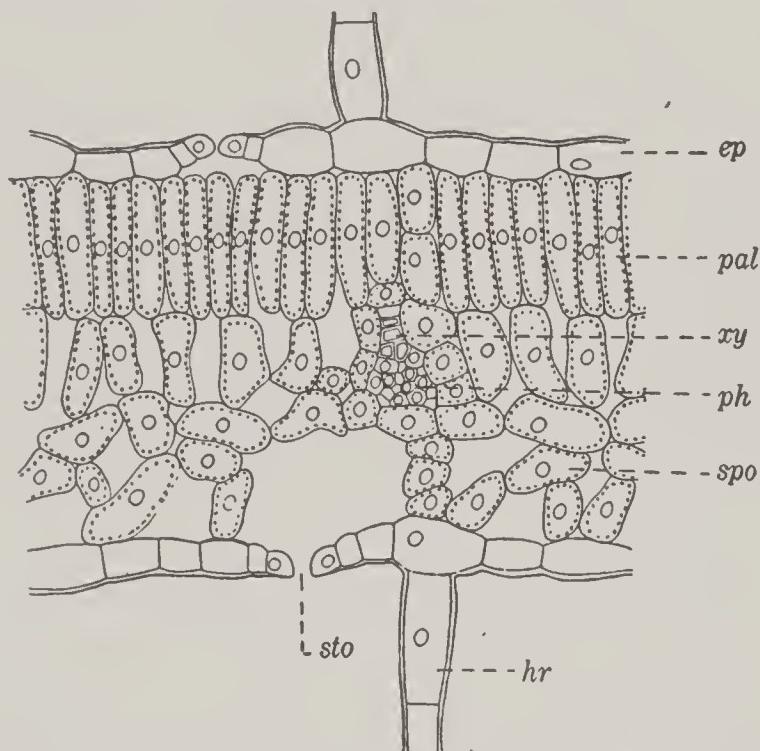


FIG. 28. Transection through a portion of the blade of the tobacco leaf: *ep*, epidermis; *br*, epidermal hair; *pal*, palisade cells; *ph*, phloem; *spo*, spongy parenchyma; *sto*, stoma; *xy*, xylem.

The mesophyll is usually differentiated into *palisade* and *spongy* cells; but in some cases it consists of parenchymatous cells that are more or less uniform in size, shape, and arrangement (*Zea*, *Lactuca*). Where differentiation exists, the palisade zone lies immediately below the adaxial epidermis, consisting of one, sometimes two, or infrequently more, layers of cells which are compactly arranged with their long axes at right angles to the surface of the blade. The palisade cells are more compactly arranged than are the spongy cells, but there are more intercellular spaces in this region than are ordinarily shown in transections of a leaf. The cells of the spongy parenchyma are approximately isodiametric and

loosely arranged, with intercellular spaces that form a system of air passages that are continuous with the substomatal cavities. Both palisade and spongy cells are chlorenchymatous, the number of plastids usually being greater in the former; and chloroplasts also occur in the guard cells of the epidermis. The border parenchyma, adjacent to the vascular elements of the smaller bundles and to single tracheids, may be lacking in chlorophyll.

The veins resemble the vascular bundles of the stem with respect to their primary tissues; and, in most instances, consist of collateral bundles that are oriented so that the xylem lies toward the adaxial surface. In plants which have bicollateral stem bundles, such vascular organization may also occur in the leaf; but it is commonly wanting in the lateral veins and in the peripheral portions of the main ones. (Fig. 29.) The secondary veins are progressively smaller with fewer vascular elements; and, ordinarily, phloem elements do not occur in the ultimate veinlets which consist of one or two xylem elements, usually tracheids, accompanied by non-chlorophyllose parenchymatous cells. Such cells presumably serve in translocation as a connecting link between the photosynthetic cells of the mesophyll and the phloem of the larger veins. The occurrence of a cambium is not uncommon in the main veins; and, in some large leaves, there may be a considerable amount of secondary vascular tissue. Associated with the main veins as a bundle sheath, or occurring as strands which parallel the veins along the adaxial and abaxial surface, are the mechanical tissues which strengthen the framework of the petiole and blade. These sclerenchymatous elements are similar to those described for the stem, consisting of elongated cells with thickened walls.

In addition to the principal tissues noted, special glandular structures may develop in the mesophyll (*Gossypium*), and lactiferous cells and ducts may be differentiated (*Lactuca*). Cystoliths (*Cannabis*) and cells containing crystalline substances and mucilages also occur.

ONTOGENY OF THE LEAF. — Ontogenetic studies of the leaf have been few, and it is only within recent years that interest in this neglected phase of developmental anatomy has been renewed. Following the classical studies of Trécul (39), Eichler (13), Hanstein (25), and others of that period, little significant work on leaf ontogeny was published until the first part of this century, except for the contribution by Lund (27) to which Foster (18) recently

directed attention. The latter (19) has also reviewed the literature on leaf ontogeny in the angiosperms and has accompanied it with an extensive bibliography. On the basis of the work that has been

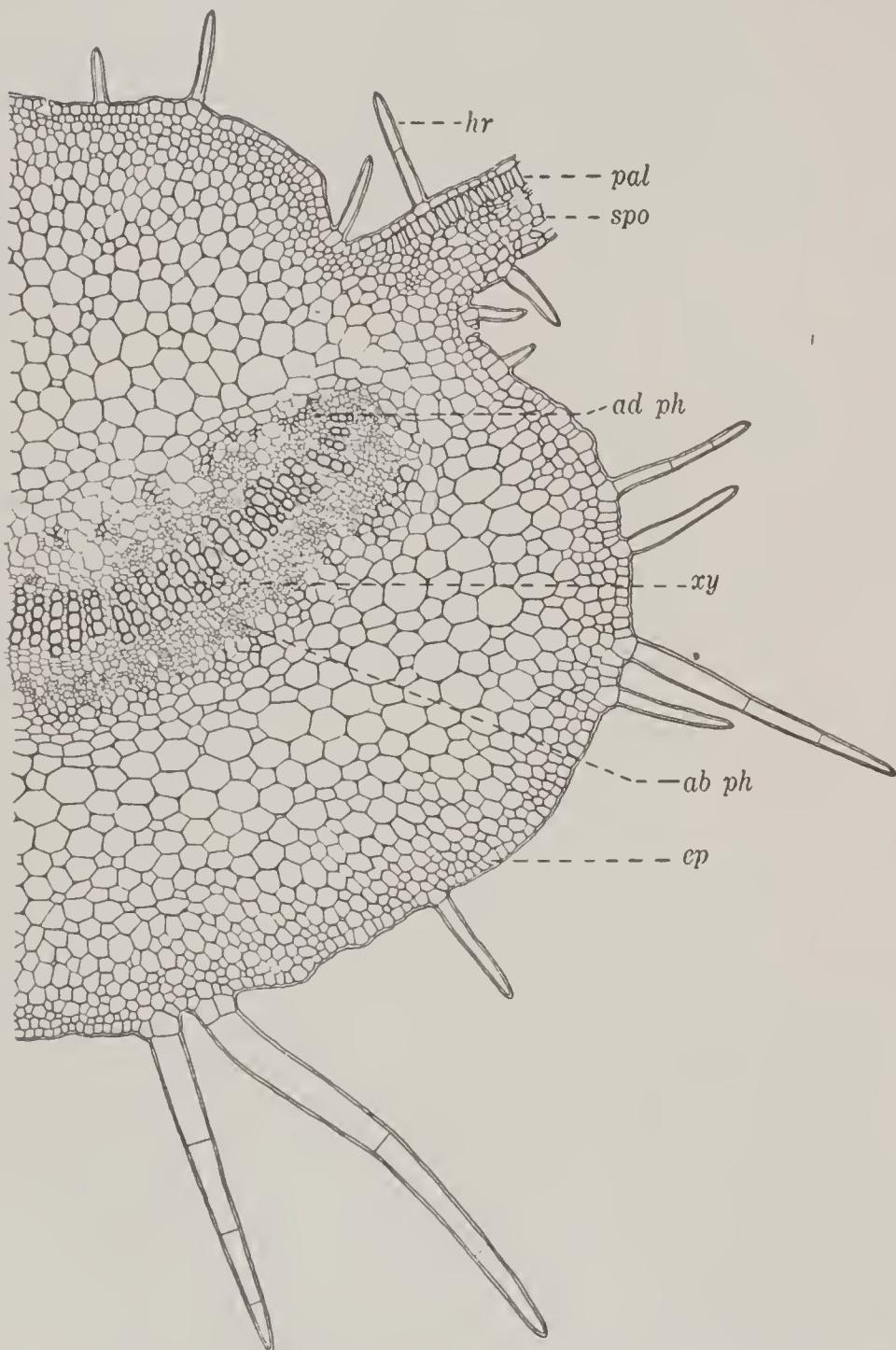


FIG. 29. Transection through the midrib of a tobacco leaf: *ab ph*, abaxial phloem; *ad ph*, adaxial phloem; *ep*, epidermis; *hr*, epidermal hair; *pal*, palisade cells; *spo*, spongy parenchyma; *xy*, xylem.

reported, it is clear that the development of the leaf in the angiosperm does not conform to any one pattern. The specific details, concerning a relatively large number of angiosperms, show no

general uniformity in the details of development, and there is a lack of agreement as to the terminology applied in ontogenetic descriptions. For this reason, it seems desirable to summarize briefly the situation with respect to nomenclature before discussing the details of leaf development.

Hanstein (25) applied the same terminology to the meristematic tissues of the stem tip as to the root tip, with the exception of the calyptrogen; and described the former as being organized into a dermatogen, periblem, and plerome. According to his account of leaf development, lateral members originate below the tip of the growing point where definite groups of meristem are formed involving elements of both the dermatogen and periblem. Subsequent divisions of the dermatogen are anticlinal only so that it forms a continuous, single layer covering the leaf, which later develops as the epidermis. The underlying cells of the periblem, by divisions in all planes, develop the tissues of the mesophyll, including the vascular bundles. The plerome of the stem axis does not enter into the formation of the lateral structures, either leaf or branch.

More recent studies indicate that there are exceptions to this type of ontogeny; and that the number of layers of meristematic cells which may be involved in leaf development is variable, ranging from one to several. Rösler (31) found that the leaf of *Triticum* develops entirely from the dermatogen, and Priestley and his associates (29) observed periclinal divisions in the dermatogen as well as underlying layers in some of their studies. On the other hand, subepidermal layers of the apical meristem of the shoot may be responsible for the development of the leaf tissues with the exception of the epidermis, and several different types of subepidermal activity have been reported. In some instances, the third layer of cells appears to be responsible for the development of the midrib or a portion of it, while the remainder of the mesophyll arises from the subepidermal layer. In *Linum*, the leaf primordium involves at least the three outermost layers, according to Crooks (9); while in tobacco, Avery (5) states that

"the leaf arises as a lateral projection of the embryonic stem tip. Its initial impetus for development comes from a few localized dividing and enlarging cells in the outer layers of the promeristem, in the portion which becomes the periblem, and still later cortex."

Because of the difficulty in following the ontogeny of the leaf on the basis of the histogens as used by Hanstein (25), Schmidt (33)

has proposed two more inclusive terms to be applied in describing the early stages. According to his concept, the apex of the shoot consists of one or more peripheral layers which perpetuate themselves by continued division, collectively termed the *tunica*. Within the tunica is the inner core of the growing point which he has designated the *corpus*. The essential distinction between the two regions is based upon differences in their manner of cell division. The cells of the tunica divide anticlinally to perpetuate its layers, and in periclinal planes only during leaf or bud formation. The

cells of the corpus, on the other hand, divide in all planes and thus increase the volume of the growing point. These terms have been rather generally adopted in recent literature on leaf development, and their use appears to be logical, since it is now established that periclinal divisions may occur in the peripheral or dermatogen layer as well as in those which underlie it. Under this system of nomenclature, the number of layers of the tunica is variable, depending upon the plant under consideration. It commonly consists of one, two, or three layers. In some plants, leaves may arise exclusively from the tunica; in

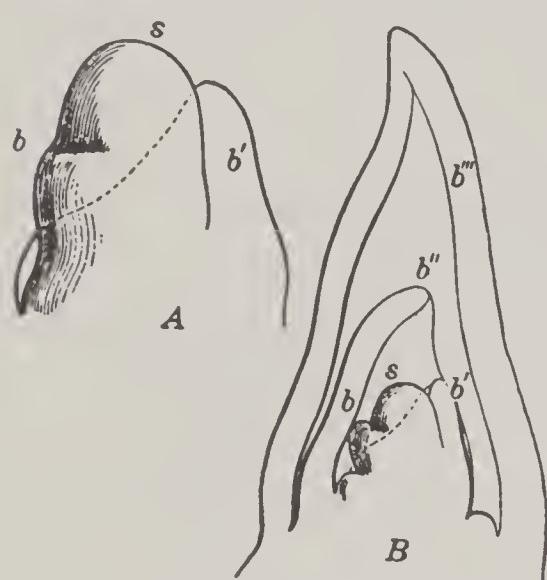


FIG. 30. The apical region of two primary shoots of *Zea* showing apex of a very small vegetative cone from which the leaves b , b' , b'' , and b''' arise as multicellular protuberances which soon surround the stem. In the axil of the leaf, b'' , is a rudimentary bud. (After Sachs, *Textbook of Botany*, Clarendon Press.)

others the internal tissues of the leaf are derived from the corpus; and an intermediate condition may exist in which the cells of both the tunica and corpus are involved in the differentiation of the leaf.

In the development of the primordium, the first evidence of its differentiation is associated with the formation of small aggregates of procambial cells. The occurrence of these zones of meristematic tissue precedes the development of any actual protuberance, and results in a transverse expansion of the stem apex to form what Louis (26) has designated as *foliar buttresses*, confirming the theories of Grégoire (23, 24). (Fig. 30.) From these buttresses, the primordia emerge, indicating the intimate relationship between

the stem and leaf, and emphasizing the earlier statement of Sachs (32), that

"the morphological conceptions of stem and leaf are correlative; one cannot be conceived without the other . . . in other words, the expressions stem and leaf denote only certain relationships of the parts of a whole — the shoot."

In connection with the actual extension of the leaf primordium from the surface of the stem apex, Schüepp (36) has pointed out that the frequency of cell division is approximately the same in all portions of the shoot apex. In other words, the number of cell divisions of the cells of the tunica would be approximately the same as those in the corpus. Since the divisions in the corpus occur in all planes, while those of the tunica are anticlinal, except during the formation of a leaf or bud primordium, the development of both regions produces folds in the superficial tissues or tunica as a necessary adjustment to the differences in the manner of cell division of the two regions.

In the development of the leaf at the foliar buttress or node, the first stages in ontogeny result in an elongation of the primordium so that it frequently becomes a tapered cone that is somewhat flattened on its adaxial surface. As Avery (5) and others have pointed out, this growth in length is apical and results from continued periclinal and anticlinal divisions of a subepidermal cell or cells. The apical growth is not limited to subepidermal cells in all cases, and subapical growth has also been reported; so that, again, it is clear that there is no strict uniformity in the ontogeny of the leaf of angiosperms. In most cases, apical growth is retarded or ceases altogether early in development, and the ensuing extension of the primordium is due to intercalary activity in addition to some unlocalized cell division which may result in an increase in the radial thickness of the primordium. It has been found that the broadening of the base of the leaf and the early development of the petiole in many dicotyledonous leaves is the result of the activity of meristematic tissues lying on the adaxial surface of the leaf base. The development of the lamina, which follows the formation of the petiolar midrib region, is initiated by the activity of marginal ridges of meristem that develop on the terminal and adaxial portion of the primordium.

Variations occur with respect to the layers involved in the production of the marginal meristems that form the young blade.

In some cases, it has been shown that the development of the blade results from the activity of a band of marginal cells which are located along the edge of the midrib; while, in others, additional underlying layers, as well as the subepidermal ones, are involved in the development of the lamina.

The characteristic thinness of the blade of foliage leaves can be related to its ontogeny. There is a relatively constant number of layers of meristematic cells in the embryonic blade, ranging from five to eight; and, from these layers, the epidermis, mesophyll, and vascular tissues of the mature blade are differentiated. Examples of the meristematic layering in the young lamina include the bean and sweet potato with six layers, and tobacco with six or seven. From these layers, the mature tissues of the leaf are derived in a definite cellular succession which is essentially constant for a given species.

In general, the upper and lower layers function as dermatogen, producing the upper and the lower epidermis respectively. The adaxial subepidermal layer develops the palisade parenchyma; the middle layer or layers produce the provascular strands, and ultimately the vascular tissue; and the abaxial subepidermal layer produces the major portion of the spongy parenchyma. Modifications in this sequence of cell lineage occur, depending upon the number of initial cell layers in the embryonic blade. In some cases, derivatives of the middle layers form a part of the spongy parenchyma, in addition to producing the vascular system; and, where a double palisade occurs, they may form a portion of that region.

The specificity of the initial cell layers of the young leaf with respect to the tissues ultimately derived from them has long been recognized and three generative layers corresponding to the three histogens of the stem were outlined by Flot (14) and Gravis (22). On this basis, the formative layers of the lamina were designated by Schüepp (36) as *protoderm*, giving rise to epidermis; *ground meristem*, producing the parenchymatous tissues of the mesophyll; and *procambium*, from which the vascular tissues are formed. The growth of the blade in surface area is due to the activity of what he has termed *plate meristems*. This activity follows the marginal growth of the lamina and continues long after the latter has ceased. Marginal growth is not discontinued simultaneously in all parts of the leaf; and, in the basipetal type of development, the

inhibition of the marginal meristem proceeds from the apex toward the base. The activity of the plate meristems consists essentially of anticlinal divisions in the respective layers so that no pronounced thickening of the blade results except in the region of the procambial strands. Differential rates of cell division and cell enlargement occur in the various tissues of the developing leaf. The palisade cells continue division after the cells of the spongy parenchyma have stopped dividing, and cell enlargement usually continues longest in the epidermal cells. These factors create stresses which account for the schizogenous formation of air spaces in the mesophyll.

The significant stages in the ontogeny of a simple foliage leaf may be summarized as follows:

- (1) The development of a meristematic primordium at the foliar buttress.
- (2) The extension of the primordium by apical and intercalary growth to form the petiolar and midrib region.
- (3) The development of the lamina by marginal meristems.
- (4) The differentiation of the tissues of the lamina from marginal and submarginal initial layers — protoderm, ground meristem, and procambium.
- (5) The surface growth of the lamina owing to the activity of plate meristems.

ONTOGENY OF COMPOUND LEAVES. — The foregoing account is based upon the development of simple leaves. The situation with respect to the differentiation of compound leaves has been less thoroughly investigated. In general, the leaflets or lobes of leaves arise in basipetal succession, from the apex toward the base; in acropetal succession, from the base toward the apex; or in what Troll (40) has termed a divergent sequence in which intermediate leaflet primordia first develop, and additional leaflets form both acropetally and basipetally from that point. An example of the acropetal method of development has been described by Sachs (32) for the Umbelliferae. In this instance, the initials of the leaflets arise at the base of the cone-like primordium of the leaf, and grow apically in the same manner in which the central portion of the leaf primordium develops. Secondary leaflets are formed in a similar way in cases where the leaf is bipinnately compound. (Fig. 31.) Foster (16, 17) has made a study of the ontogeny of the leaf of *Carya* in which the development is also acropetal.

DEVELOPMENT OF STIPULES. — Stipules may be considered morphologically as integral portions of the leaf, but relatively little work has been done in regard to the details of their development. Early studies on stipules were concerned primarily with speculation as to the relation of the stipule to the leaf; and, more particularly, the consideration of any evidence based on the presence or absence of stipules which might serve as an aid in phylogenetic interpretations. Considerations of this nature have been reported by

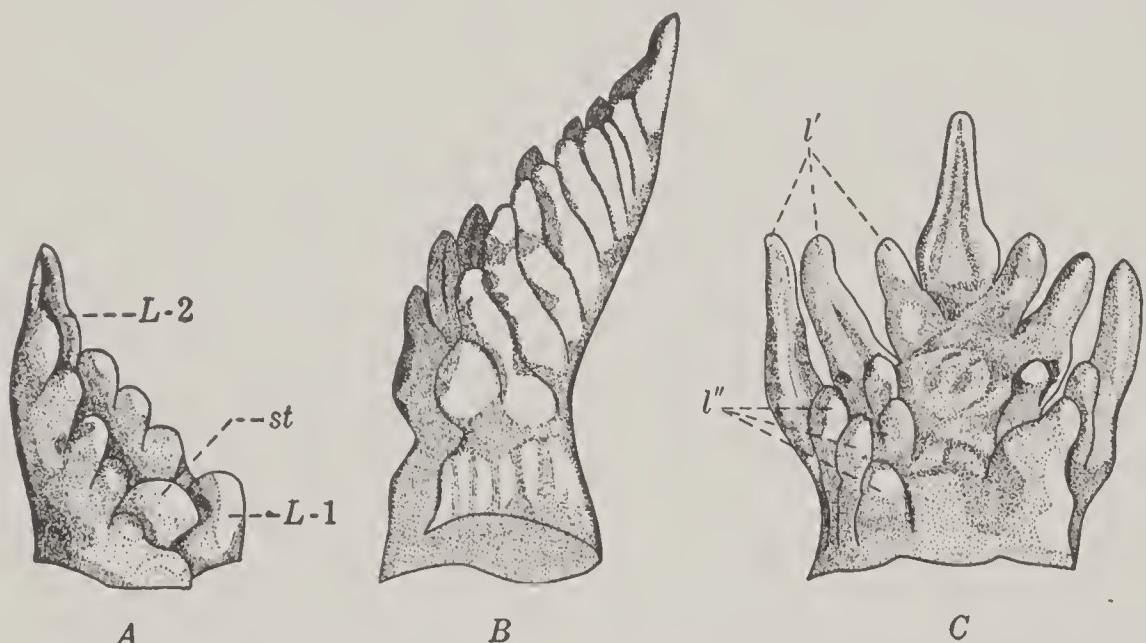


FIG. 31. Development of the pinnate leaves of the Umbelliferae. A, B, of *Pastinaca sativa*; C, of *Levisticum officinale*. In A, the stem tip and youngest leaf *L*-1 are shown. The leaf, *L*-2, has commenced pinnation. In B, the primary pinnation of a single leaf is shown. In C, the leaflets of the first order, *l'*, have given rise to secondary leaflets, *l''*; *st*, stem tip. (Redrawn and adapted from Sachs, *Textbook of Botany*, Clarendon Press.)

Domin (12), Sinnott and Bailey (38), Schrödinger (34), and more recently by Ponzo (28).

Ontogenetic studies have been limited, and have received but brief mention in connection with general foliar studies. Cross (10) has described the development of the stipules in *Morus alba* and states that they "undergo a decidedly different ontogenetic development from that of the foliage leaf, but they exhibit certain features of development which are strikingly suggestive of bud scale histogenesis." Following expansion, stipules sometimes absciss early, before the foliage leaf attains its full size. Abscission is not a constant character of these structures; for, in many cases as in *Pisum*, they are not only persistent, but perform an important role in photosynthesis.

DEVELOPMENT OF BUD SCALES.—Like the stipule, the bud scale or cataphyll has received relatively little attention from the ontogenetic point of view, the principal references to it being concerned with its relation to phylogeny and speculation with respect to theories of recapitulation and metamorphosis. Certain generalizations can be made regarding the principal anatomical differences between the bud scale and the foliage leaf. (1) Stomata are reduced in number or may be entirely lacking; and, when present, are more numerous on the adaxial surface of the scale than on the abaxial one, which usually has a heavy cuticle. (2) There is a reduction in the amount of mechanical tissue of the collenchymatous type. (3) There is usually a reduction or complete absence of palisade tissue; and the parenchymatous cells are homogeneous with fewer air spaces than are found in the spongy parenchyma of the foliage leaf. (4) There is a definite reduction in the amount of vascular tissue, the number of xylem and phloem elements is reduced, and the former are less strongly lignified.

Considerable interest attaches to the question as to what factors determine whether a foliar primordium will develop as a cataphyll or as a foliage leaf. Goebel (21) has regarded the cataphyll as developing from a foliar primordium which is arrested in its developmental stages and as a result pursues a divergent ontogeny leading to the differentiation of a bud scale. Objections to this "transformation" theory have been raised by Schüepp (37) and Foster (15), the former showing that the character and position of the meristematic tissue, and the rapidity of its maturation, are important factors in determining the ultimate development of a foliar primordium. Foster has suggested that there is a significant periodic alternation of cataphylls and foliage leaves. He has also noted differences in the character of the meristematic activity and the development of the derivative cells of the bud scale as compared with the foliage leaf.

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CHAPTER IV

THE ANATOMY OF THE FLOWER AND FRUIT

FUNCTIONALLY, the *flower* is an organ concerned with the development of the structures that lead to *gametic reproduction*. On this basis, the statement of Goebel (3) that a flower is "a shoot beset with sporophylls" is in accord with the floral function, since the stamens and carpels produce microspores and megasporangia from which the gametophytic structures arise. These, in turn, produce gametes, gametic union ensues, and the resultant zygote develops as a new sporophytic generation. It is evident from this that the flower is a sporophytic structure, and that it is a misconception to refer to the stamens and carpels as organs of gametic or sexual reproduction.

Anatomically, the flower is a shoot. On this basis, the floral axis is not unlike a vegetative one, as described in the preceding chapter, which gives rise to successive leaf primordia from a terminal meristem. The difference is not fundamentally in the manner of origin of the foliar and floral parts respectively; but, rather, in the character and function of the structures.

FLORAL PARTS. — The typical, perfect flower of the angiosperms has four types of floral leaves, *sepals*, *petals*, *stamens*, and *carpels*, which are diverged from the *receptacle* or *torus*. The two first named do not possess sporangia, and constitute the *floral envelope* or *perianth*; the other two, stamens and carpels, normally bear functional sporangia. In addition to these parts various types of *bracts* may be associated with an individual flower, as in many of the Rosaceae. The differences which distinguish the many floral types are quantitative rather than qualitative variations, since the same basic structures may be present in any given flower; but their size, number, and degree or extent of development may vary widely. There may be qualitative modification of such structures as carpels and stamens; but, this is far less common than quantita-

tive variations in the number, size, shape, and degree of divergence of these parts. On the basis of this concept, it is possible to interpret the great variety of floral structures, and to interrelate them in a logical manner.

The sepals collectively constitute the *calyx*, forming the outermost spiral or cycle of the floral axis; and the sepal often resembles a vegetative leaf in structure and venation. They are usually chlorophyllose and photosynthetic; but their primary function, at least in the early ontogeny of many flowers, is that of protection. In the bud stage, they form an enveloping structure which overarches and encloses the other floral parts prior to anthesis. Other specialized functions are attraction of insects and the dissemination of the fruit. In some instances, the calyx is entirely lacking.

The petals, collectively termed the *corolla*, comprise the second or inner set of the perianth. They may occur in one or more spirals or cycles and are often white or some color other than green. Their function is primarily that of attraction of insects, but they also serve as a protection to the stamens and carpels. In this connection, they may be specialized as to their shape, position, or habit of opening and closing. In some floral types (*Anemone*), the petals are lacking; and the sepals are brightly colored, or there may be brilliant leafy bracts (*Poinsettia*). In wind-pollinated cereals, the petals, like the sepals, are either much reduced or absent.

The stamen or *microsporophyll* consists of a stalk or *filament* and a terminal *anther* comprised of one to several (usually four) *microsporangia* or *pollen sacs*. During the development of the microsporangia, and following reduction division, microspores and eventually pollen grains (*microgametophytes*) are formed. Commonly, the wall between adjacent microsporangia is broken; so that, in the mature stamen, the anther consists of two locules or pollen chambers instead of four separate microsporangia. These pollen sacs dehisce in various ways at maturity, and the pollen may be exposed or liberated through terminal chinks or pores, or by means of a splitting of the anther wall.

The carpels or *megasporophylls* constitute the central or terminal set of floral structures, and are referred to singly or collectively as a *pistil*, or the pistils. The pistil may be *simple* consisting of a single carpel, or *compound* if it is made up of two or more carpels.

Three distinct parts usually comprise the pistil, the basal *ovary*, the more or less elongated *style*, and the *stigma*, which is terminal or lateral in greater or lesser degree. The receptive surface of the *stigma*, upon which the pollen grains lodge and initiate growth of the pollen tube, may be papillate or plumose and feathery. In many cases, glandular hairs provide a sticky secretion which stimulates growth of the pollen. The entire carpel, or some portion of it, constitutes the true *fruit*, and the seeds are developed and contained within it. In many cases, other structures are associated with it at maturity, and the assemblage is called the fruit.

FLORAL ONTOGENY. — In the ontogeny of the flower, the primordium first appears as a rounded growing point of meristematic tissue. From this, the primordia of the floral parts arise as lateral structures in a spiral or series of cycles and develop much in the manner of foliar primordia, expanding and developing vascular traces. The subsequent development of the floral axis differs from that of a vegetative one in that there is little internodal elongation, so that the floral parts mature in a compact relationship rather than being more or less widely separated from one another.

In flowers that are regarded as relatively primitive, the origin of the floral primordia in an acropetal succession results in the development of the *hypogynous* flower. (Fig. 32.) In a cyclic flower of this type, each successive cycle is definitely above and centrad to the next outer cycle; and the level of divergence of the stamens, petals, and sepals is below that of the carpels.

In many flowers, development involves some degree of *zonal growth*. Instead of each part differentiating as a separate entity, there may be an activation of a whole zone of meristematic tissue with varying degrees of subsequent divergence or differentiation of individual members. Where this tendency toward zonal growth is expressed *perigynous* or *epigynous* flowers are formed.

In *perigyny*, the elongation of the terminal portion of the floral axis which gives rise to the carpels is inhibited, and the outer cycles of the growing point develop as a zone so that the three outer sets of floral parts grow conjointly at their bases and are diverged from the rim of an urn or cup-like outgrowth as separate structures. This makes it appear that the carpels arise from a depression in the torus or receptacle; but it is actually the result

of two factors, the differential growth rate of the cycles of floral primordia, and zonal or partial conjoint growth of the outer cycles. (Fig. 33.)

In *epigyny*, differential and zonal growth occur to a greater degree and the apical growth of the morphological end of the floral axis is inhibited. The zonal growth of the outer cycles forms

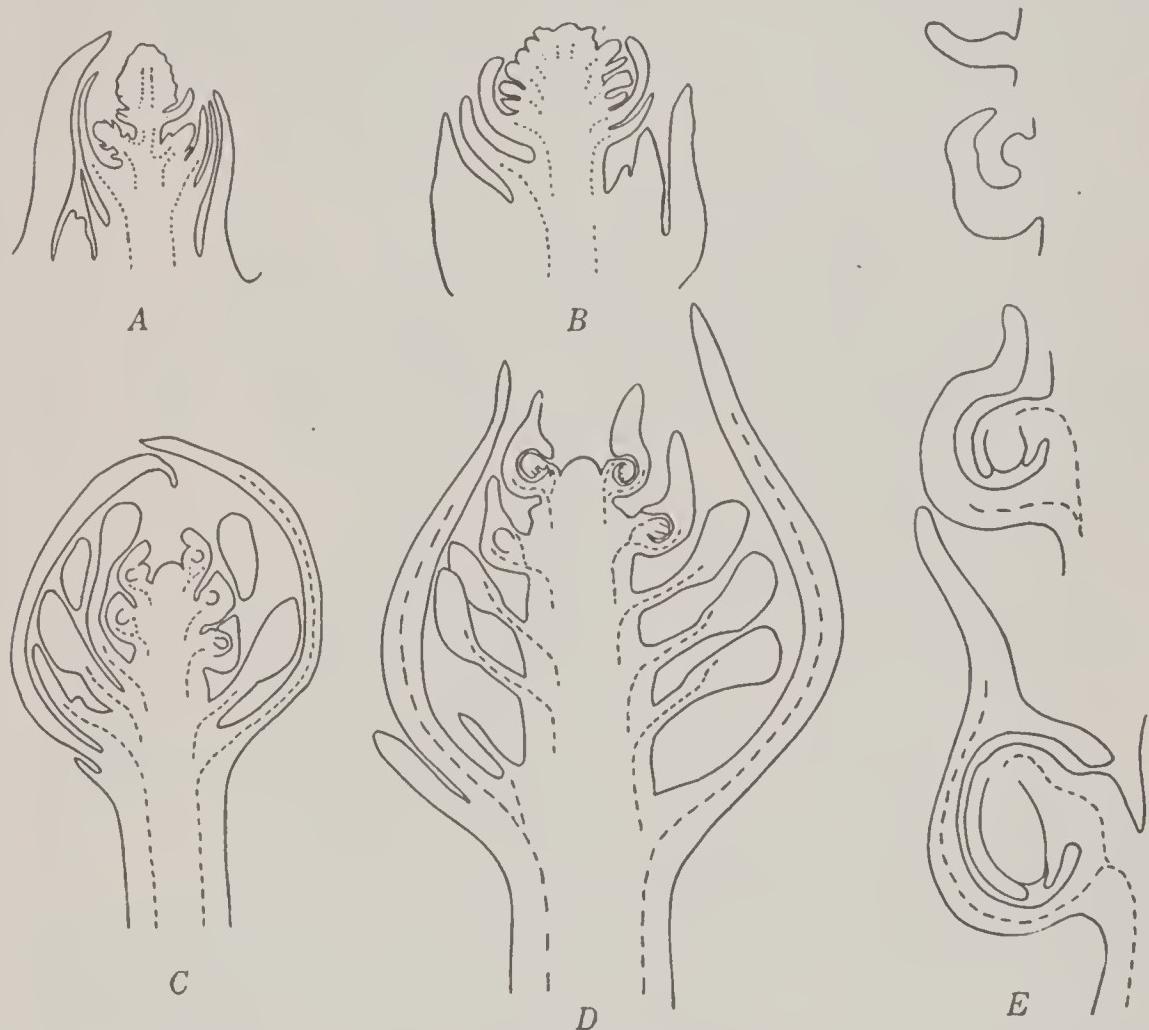


FIG. 32. *Ranunculus*; development of the hypogynous flower. *A*, the floral axis with terminal primordium and two lateral floral axes; *B-D*, progressive stages in the ontogeny of the flower; *E*, four stages in the development of a carpel and the single ovule.

an enclosing structure which is non-diverged from the walls of the ovary. The styles, stamens, petals, and sepals are then diverged as separate structures from the top of this common zone of tissue; or there may be further expression of non-divergence, a common case being that in which the corolla is a tubular structure of non-diverged petals. Many intermediate stages between hypogyny and complete epigyny occur in floral development, and this again points to the fact that differences in floral type are more of a quantitative nature than qualitative. (Fig. 34.)

In many instances, the individual members of a given whorl do not arise simultaneously but in succession. This is illustrated in the papilionaceous Leguminosae (*Pisum*), where the abaxial sepal arises first, followed by the two lateral ones; and, finally, the two adaxial lobes. Similarly in the corolla, the two petal primordia which form the keel are the first to arise, followed by the two lateral primordia forming the wings; and, lastly, by the primordium of the standard. In other cases, it has been demonstrated

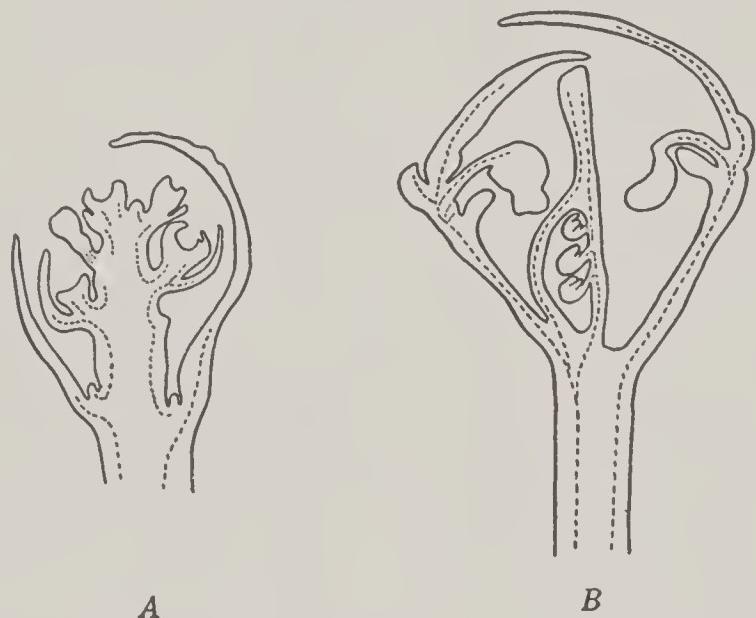


FIG. 33. A, the floral branch of *Spiraea*; B, a young flower showing perigyny.

that the sequence in a given cycle may be progressive in a counter-clockwise or a clockwise spiral.

Many exceptions to the acropetal mode of development are known. In certain Compositae, the much reduced or modified sepals do not appear until after the differentiation of the stamens and carpels; and in some of the Cruciferae, the petals are the last primordia to appear. Instances have been observed in the Rosaceae in which the succession of development is sepals, inner stamens, carpels, outer stamens, and petals; while in other members of this family, the primordia of the carpels appear before the full quota of stamens has been determined. This indicates that there are exceptions to true acropetal succession and that the actual appearance of the floral organs may be in part basipetal and in part acropetal or irregular. In some cases, these apparent irregularities can be interpreted as a delayed enlargement of potential primordia or a non-divergence of parts of a cycle or adjacent cycles. For example, in the Primulaceae the petals appear late in ontogeny after the

stamens; and, as Coulter and Chamberlain (1) point out, this may be interpreted "as a case in which the primordia of stamen and petal have a common origin, entirely analogous to the sympetalous corolla with stamens 'inserted on its tube,' but in which the

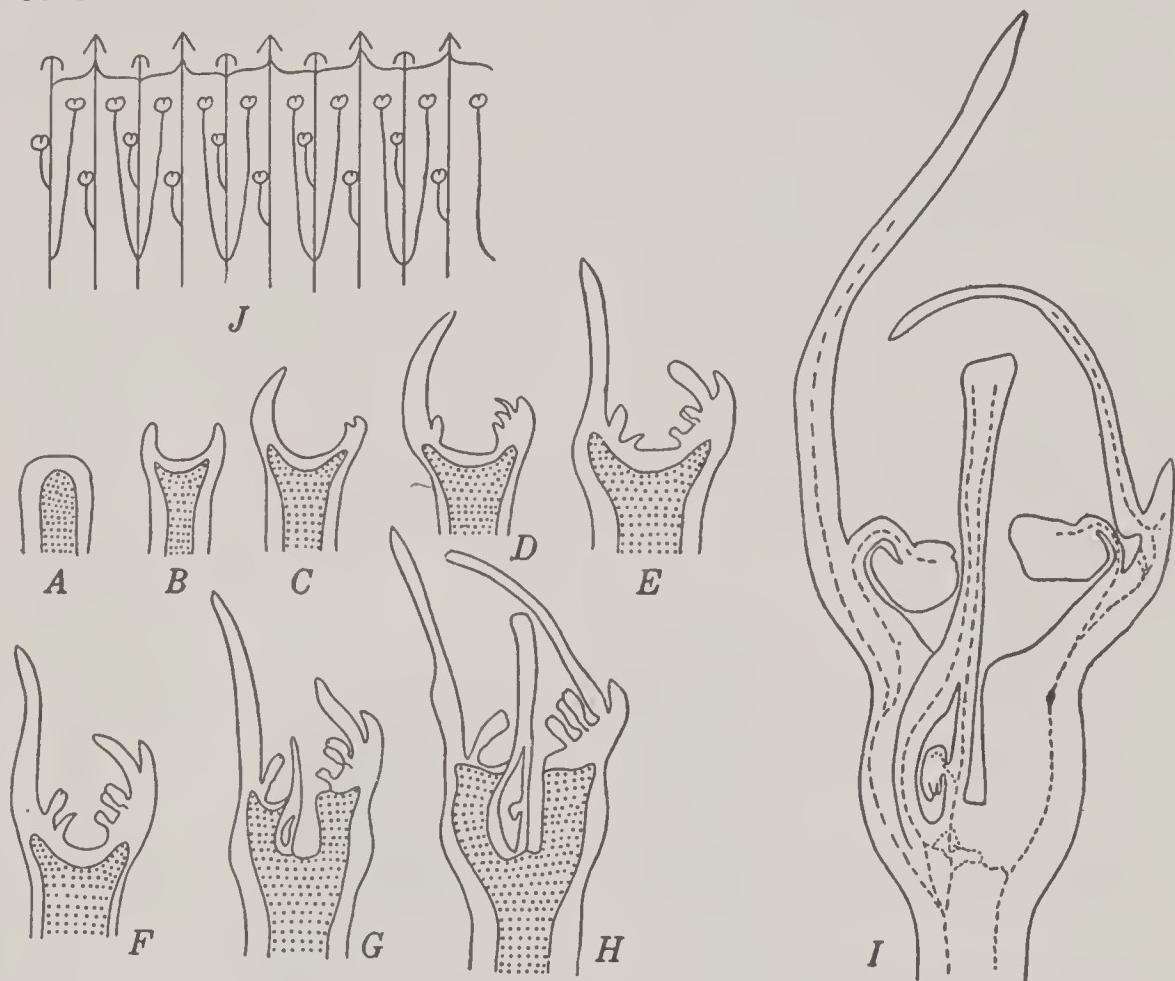


FIG. 34. A-H, stages in the development of the flower of the apple showing epigyny. The stippled regions indicate the pith of the axis. I, a young flower bud showing epigynous character and vascular system. J, diagrammatic representation of the vascular system of the apple. (Redrawn and adapted from Kraus.)

separate primordia of the petals have been delayed in their appearance."

The character of the symmetry of a flower also constitutes a point of variation. In the *actinomorphic* forms, the parts of the flower are arranged in a radial symmetry; while, in the *zygomorphic* type, the flower is bilaterally symmetrical and can be divided in only one plane of symmetry. The former occurs in the majority of cases, while the latter more specialized type is represented in many legumes, including *Pisum* and *Medicago*.

In contrast with the view that the vegetative and floral axes are fundamentally alike, and that the foliar and floral organs are similar in the initial stages of their development, Grégoire (7)

holds that the growing points of the two axes are different, and that no homology between foliar and floral organs exists. He concludes that the theory of metamorphosis does not apply in any way to the flower, and that it is an autonomous structure. For this reason, he dissents from the idea that the floral organs are sporophylls, and suggests that the stamens be termed "microsporangiophores," and the carpels "spermatophores."

THE INFLORESCENCE. — In addition to variations in the structure of individual flowers, the character of the inflorescence may

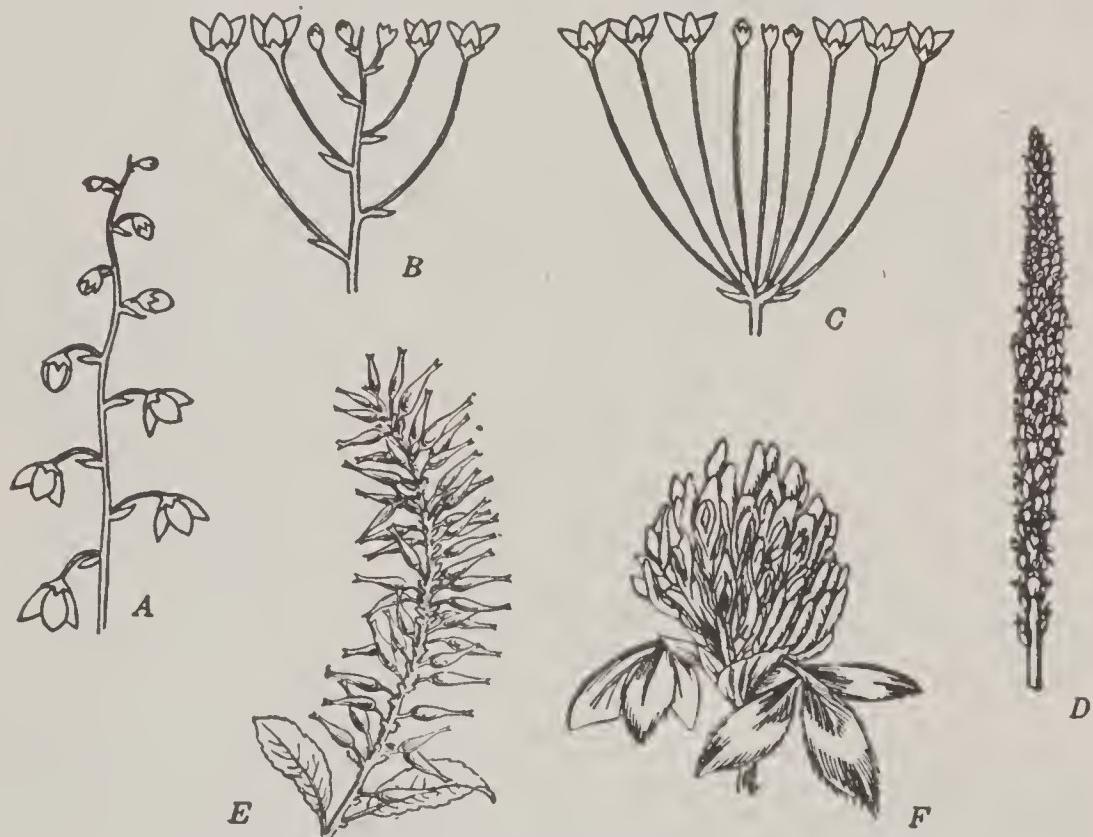


FIG. 35. Types of inflorescences. *A*, raceme (diagrammatic); *B*, corymb (diagrammatic); *C*, umbel (diagrammatic); *D*, spike of plantain, after Bailey; *E*, catkin of willow; *F*, head of clover, after Smalian. (From Smith, et al., *Textbook of General Botany*.)

be distinctive. Flowers occur separately in a terminal or axillary position; or, more commonly, form a flower cluster in which they are more or less closely arranged with reference to one another. The development of the inflorescence may be *monopodial* or *sympodial*. In the monopodial development, the inflorescences are indefinite, and result from the formation of a series of branches which arise from the main axis in acropetal succession. Where the lateral branches do not rebranch, the inflorescence may be a *spike* or *raceme* if the main axis is elongated; or a *head* or *simple umbel* if it is unelongated. (Fig. 35.) In the *spike*, the flowers are

sessile on an elongated axis as in the carpellate flowers of *Cannabis*. In the *raceme*, the flowers are pediceled on an elongated axis rather than being sessile like the spike (*Raphanus* and *Medicago*). In the *head*, the sessile flowers are closely aggregated on a shortened axis (*Lactuca* and most *Compositae*). In the *umbel*, the lateral axes bearing the flowers are approximately equal in length, each one terminating in a flower.

Where the lateral branches rebranch and each axis is terminated by a flower, a *panicle* is formed. (Fig. 36.) Included in this category are the true *panicle*; the *compound panicle*, or spike made up of spikelets (*Triticum*); and, where the main axis is unelongated,

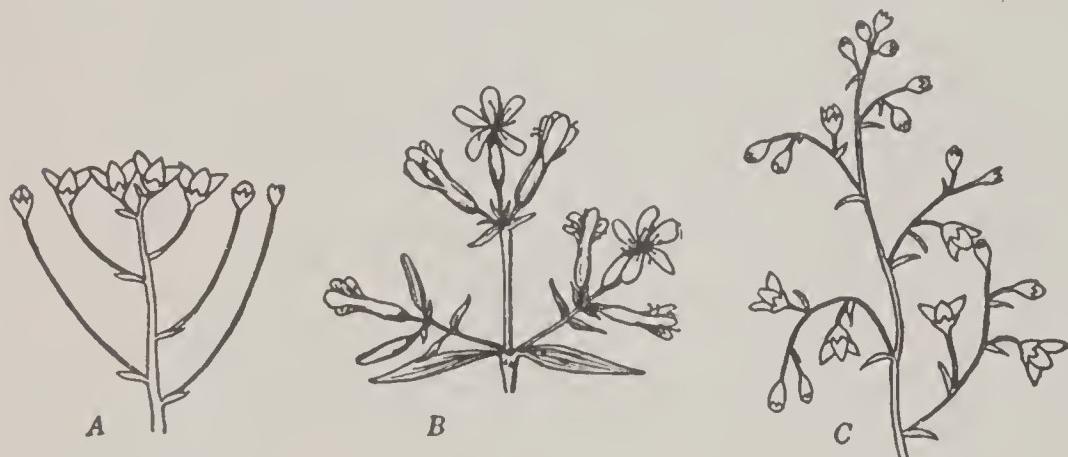


FIG. 36. Types of inflorescences. A, cyme (diagrammatic); B, compound cyme of *Saponaria*, after Rushby; C, panicle (diagrammatic). (From Smith, et al., *Textbook of General Botany*.)

the *compound umbel*. In the *compound umbel*, each lateral axis is terminated by a small *umbellule* bearing several flowers (*Apium* and other members of the *Umbelliferae*). In the *cyme*, the branching is sympodial and determinate. The inflorescence is usually broad and flat, and the lateral axes terminate in flowers after producing one or more branches of a second order which also bear flowers (*Linum*).

FLORAL TYPES AND PHYLOGENY. — The possibilities of variation in floral types are almost unlimited. The most obvious of these are variations in the color of the flower, and in the size, shape, arrangement, and number of floral parts. Where the flowers are cyclic, the most common floral plan is the *pentacyclic* one, in which there are five sets of parts, these usually consisting of one cycle of sepals, one of petals, two of stamens, and a central cycle of carpels. In the *tetracyclic* arrangement, there is only one cycle of stamens. Where the number of carpels is the same as the number of sepals and

petals, the flower is regarded as *isocarpic*, and when the number of carpels is less than that of the other floral parts, it is said to be *anisocarpic*.

In applying the facts of floral development and structure to phylogenetic interpretation, certain characteristics have come to be regarded as representing relatively high evolutionary position, while others seem to be indicative of primitive rank. In a general way, the following table indicates some of the high and low characters.

TABLE I

RELATIVELY LOW OR PRIMITIVE CHARACTERS	RELATIVELY HIGH OR ADVANCED CHARACTERS
Spiral arrangement of floral parts	Cyclic arrangement of floral parts
Distinct parts	Undiverged parts
Indefinite, usually large numbers of parts	Definite numbers of parts
Pentacyclic flowers	Tetracyclic flowers
Hypogyny	Epigyny
Isocarpy	Anisocarpy
Actinomorphy	Zygomorphy

VASCULAR ANATOMY OF THE FLOWER. — The divergence or non-divergence of the floral parts is commonly associated with a divergence or non-divergence of the vascular bundles which supply these parts; and, in the last analysis, the interpretation of the floral structures may rest upon their vascular anatomy. In simple types, with a regular acropetal succession, the floral parts diverge one above the other, in the same manner as foliage leaves, and each floral structure has a distinct vascular bundle or bundles. In types where there is a non-divergence of floral parts, there may be an accompanying non-divergence of the vascular system; and, in some instances, this reaches a point where it is not possible to distinguish between the stem tissue and the conjoint floral structures. This situation occurs in many perigynous and epigynous flowers. In the apple, for example, where the receptacle grows up around the carpels, there is no delimitation between the carpels and the stem. Vascular reduction of this type is generally associated with advanced floral types, and non-divergence of the vascular system is considered an advanced evolutionary character.

In general, the primary vascular supply to a sepal consists of the same number of bundles as supply the foliage leaf of the plant.

Each petal and stamen is ordinarily supplied by a single bundle, and the number of major bundles supplying a carpel is normally three, one abaxial and two adaxial. These are frequently modified, especially in compound pistils where adjacent adaxial bundles may anastomose. In some instances, the abaxial bundle may appear to be a double bundle (*Pisum*), owing to the development of a bisecting parenchymatous ray.

MICROSPOROGENESIS. — The initial protuberance of the primordium of a stamen develops into two parts, the terminal *anther* and the *filament*. In the anther, the cells are at first uniform, except for the epidermis; but, a little later, the cells of the provascular strand are differentiated, and a hypodermal cell or a group of them appear which have a denser cytoplasm and can be distinguished from the adjacent cells on this basis. These are the *archesporial cells*, although the whole hypodermal layer may be regarded as having archesporial potentialities. The number of cells which are functional is ordinarily limited, and their subsequent development results in the formation of the lobed regions of the anther. They occur in longitudinal rows; and, in a transection of the anther, may appear as a single cell or as groups of four to six or more. Cases have been reported in which a single cell may constitute the whole archesporium.

The archesporial cells enlarge and divide both radially and tangentially. The tangential divisions result in the differentiation of outer cells as the *primary parietal cells* and the inner as the *primary sporogenous cells*. From the former and their derivatives, the walls of the embedded sporangia, of which there are typically four, develop. If the cells of the primary parietal layer divide periclinally, a series of parietal wall layers of varying number is developed. The outermost wall layer constitutes the *endothecium*. It may become definitely specialized by the development of wall thickenings which are related to the dehiscence of the anther.

The innermost parietal layer or sometimes the outer sporogenous layers form the *tapetum*. Regardless of its morphological origin, the tapetum serves as a nutritive layer for the developing *microspore mother cells* and *microspores*, and it is more or less completely digested during the progress of their growth and maturation. During the development of the primary parietal cells, the primary sporogenous cells may undergo successive divisions or function directly as microspore mother cells. In either case, each microspore mother cell

undergoes the reduction divisions which result in a tetrad of microspores (young pollen grains).

Coincident with the formation of the microspores, digestion of the non-sporogenous tissues leads to the formation of the locules of the four sporangia; and, frequently, the walls between adjacent sporangial cavities disintegrate so that the mature anther contains two locules or *pollen sacs*. Dehiscence of the anther occurs in extremely varied ways. In some cases, a longitudinal splitting occurs along a definite *stomium*. In others, there is a small apical fissure, a terminal pore, or an irregular breaking of the tissues. The wall tissues of the pollen sacs are frequently hygroscopic; and when they become moist, the endothelial cells may close the stomia again, in this manner covering any pollen which has not been shed.

At the time of shedding, the pollen grains have usually passed beyond the microspore stage, their nuclei having divided to form a *tube* and *generative* nucleus. In some instances, the latter may have again divided so that at the time of shedding, the pollen grains are trinucleate. Thus the mature pollen grain may be regarded as a *microgametophyte*, which consists either of a tube and generative cell, or a tube cell and two *microgametes*.

DEVELOPMENT OF THE CARPEL. — The carpels may develop singly as in some of the Rosaceae and Leguminosae, or several of them may develop conjointly or undiverged so that the resultant pistil is compound (syncarpy). When a single simple carpel develops, the primordium of the *carpel*, or *megasporophyll*, generally arises as a more or less open structure whose margins, because of differential growth, eventually meet, leaving a slight furrow or *suture* at their junction which in some instances is complete. The basal portion of the carpel constitutes the ovary, the terminal portion of the primordium elongates to a greater or lesser degree to form the style with the stigma at its tip or along its apical margins. The *adaxial suture* represents the margin of the sporophyll, its *abaxial suture* the midrib. There is often a prominent vascular bundle extending the length of the abaxial suture, and one in each of the edges along the adaxial suture.

PLACENTATION. — The inner ridges of the carpellary margins in the ovarian portion make up the *placentae*. It is from this region that the ovule or ovules arise. In the simple carpel where the initiation of the ovules is marginal, the placentation is *parietal*. This type frequently occurs in syncarpous ovaries when the margins

of adjacent carpels form peripheral ridges which protrude from the inner surface of the wall, but do not extend centripetally to the center of the ovarian chamber. (Fig. 37, A.)

In the *axile* type of placentation, the placental tissue lies at the center of the ovary and may be foliar, or in part foliar and in part caulin, as in the tomato. In some instances, the inturned margins of the carpels extend to the center of the ovary and then are folded back toward the periphery of each locule so that they appear as projecting ridges extending from a central axis in the ovary (*Cucurbita*). (Fig. 37, B.)

The less common type is *free-central* placentation, which occurs in the Caryophyllaceae and Primulaceae. Dickson (2) has described the placental development for representatives of each family. In the former, the entire placental region consists of the fused margins of five carpels which are separated from the ovary wall by the disintegration of the intervening tissue. In this manner, a form of free-central placentation is brought about which is also referred to as "*free-marginal*" placentation. In the Primulaceae, the *free-central* placenta is interpreted

"as the fused margins of the carpels (plus or minus residual axial tissue), which are separated from the outer portions of the carpels at their origin in the receptacle, instead of breaking away after the definition of the individual carpels, as in the Caryophyllaceae." (Fig. 37, C.)

TYPES OF OVULES. — The ovule consists of a *nucellus*, sometimes called the *megasporangium*, and the *integuments* which grow over and around it. There are one or two integuments; or, infrequently, there may be none, as in some of the Amaryllidaceae.

From the placenta, a dome-shaped mass arises which develops as one of the several types of ovules. In the development of the ovule, the initial protuberance is formed by the division of cells of the hypodermal layer which form a mass of tissue, while the over-

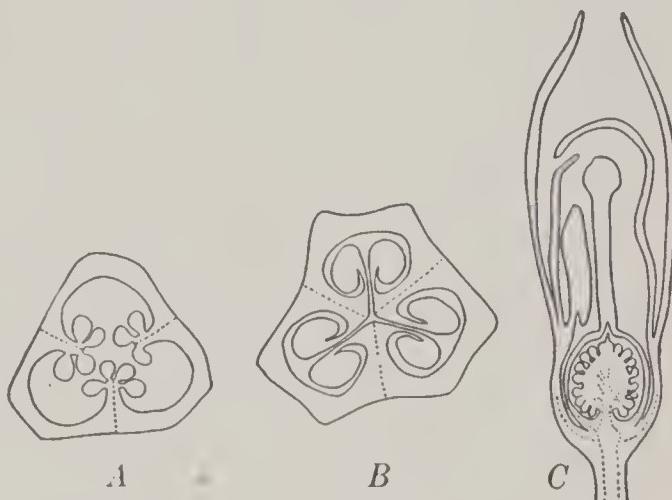


FIG. 37. Types of placentation: A, parietal (diagrammatic); B, axile (diagrammatic); C, free central, longisection of young flower of *Primula*.

lying epidermal cells divide only anticlinally to compensate for the enlargement of the nucellus. As this takes place, an annular fold arises at the base of the nucellus which becomes the inner integument. This usually grows with greater rapidity than the nucellar tissue; and, in most cases, eventually encloses it. When there are two integuments, the outer one is initiated soon after the inner is differentiated and later completely surrounds it.

In the *orthotropous* type, the ovule develops as a straight structure; and the integuments grow out and enclose the nucellus in such a way that the *micropyle* is in a straight line with the *chalaza* and *hilum*. This form of ovule is also termed *atropous*. Common examples occur in the Polygonaceae (including *Fagopyrum*, buck-

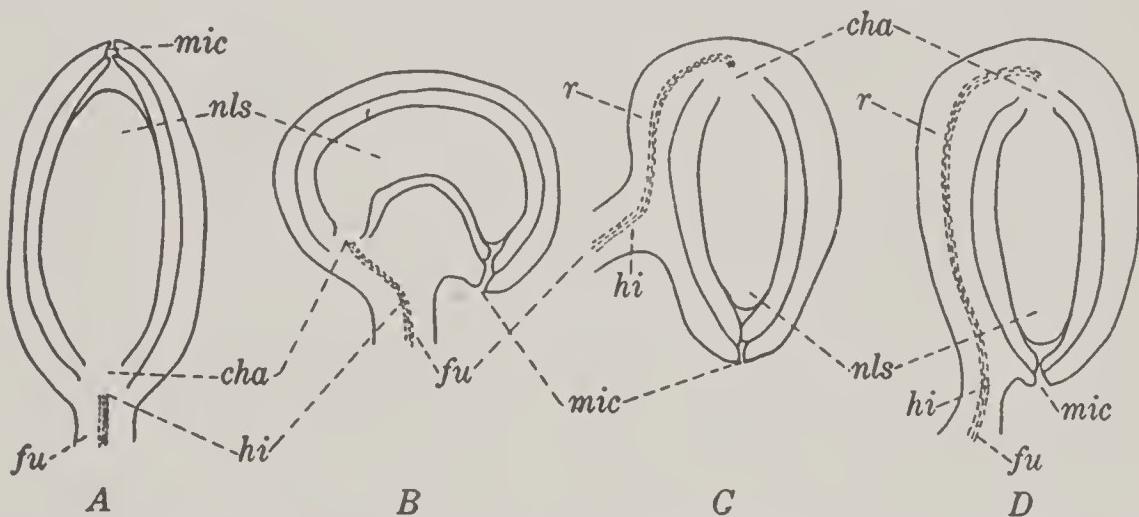


FIG. 38. Types of ovules: A, orthotropous; B, campylotropous; C, hemitropous; D, anatropous (all diagrammatic): *cha*, chalaza; *fu*, funiculus; *hi*, hilum; *mic*, micropyle; *nls*, nucellus; *r*, raphe.

wheat, and *Rheum*, *rhubarb*), in the Juglandaceae, Urticaceae, and several other families. (Fig. 38, A.)

Where the nucellus is not in a straight line with the *funiculus* but is curved or bent over in such a way that the chalaza and *micropyle* are in a plane at right angles to the funiculus, the type is known as *campylotropous*. This is common in many of the Caryophyllaceae and Berberidaceae. (Fig. 38, B.) Where the funiculus is sharply curved just below the chalaza so that the nucellus and integuments are inverted and lie alongside the stalk of the funiculus with the *micropyle* directed toward the placenta, the ovule is *anatropous*. (Fig. 38, D.)

A fourth type, *hemitropous*, which is intermediate between *orthotropous* and *anatropous*, occurs when the ovule is half inverted rather than completely so, as in *anatropous* ovules, so that the

micropyle and chalaza are at right angles to the hilum. It differs from the campylotropous type in that the nucellus is straight in this type rather than curved. (Fig. 38, C.)

Occasionally, in the development of the ovule there is a non-divergence of its parts. This results in conjoint growth of the nucellus and integuments, or conjoint growth of the funiculus and the integument. Frequently, in anatropous ovules, this leads to the development of a ridge-like structure, the *raphe*.

MEGASPOROGENESIS. — The nucellus begins its development as a more or less localized activity of the hypodermal layers of the sporophyll; and, as in microsporogenesis, the archesporial cells are hypodermal. A hypodermal cell (or several of them) constitutes the *archesporium*, becoming larger than the adjacent cells. The cells of the epidermal layer sometimes divide periclinally so that several layers may develop from it, forming an epidermal cap. The archesporium, which in most instances consists of a single cell, may divide transversely, the outer daughter cell becoming the *primary parietal cell*, and the inner one functioning as the *primary sporogenous cell*. In other cases, the archesporial cell may function directly as a *megaspore mother cell*. If a primary parietal cell is cut off, it may undergo several periclinal divisions producing wall cells, in addition to such as may have come from the epidermis. There are many variations in the behavior of the primary parietal tissue, from types in which there is a pronounced development to those in which the parietal cells undergo few or no periclinal divisions. Where there is no initial transverse division of the archesporial cell, there is no development of parietal wall tissue.

The behavior of the megaspore mother cell is markedly uniform in the angiosperms, despite the fact that several types are recorded. A linear tetrad of megaspores is formed, accompanied by reduction division. Of the megaspores, the chalazal one of the linear series is usually functional; and, as a result of successive nuclear divisions, an eight-celled megagametophyte is formed. At maturity, it consists of a *megagamete* and two *synergids*, located at the micropylar end; three *antipodals* at the chalazal end; and two *polar nuclei* which are more or less centrally located. Commonly, the polar nuclei unite just prior to or coincident with their union with one of the microgametes to form the *endosperm nucleus*. This occurs in the process of double fertilization at the time when the megagamete and microgamete unite to form the *zygote*.

THE FRUIT. — The *fruit* of the angiosperms consists of the ovary together with any closely associated parts. The ovary may be simple, as in the *akene* (buttercup), *pod* (pea), and the *drupe* (plum); or it may involve two or more carpels, as in the *silique* (radish), the *berry* (tomato), and many others. Associated structures which may be a part of the fruit in certain types include the receptacle, sepals, basal portions of the stamens, and the axis itself. In some special cases (artichoke), the floral bracts and all the floral parts may constitute the fruit if the whole head is considered as such.

There are several systems of classification of fruit. These vary, depending upon the point of view upon which the classification is based, and the characters which are regarded as determinative. On the basis of the texture of the pericarp, and accessory parts when present, fruits may be classified as being *dry* (papery, stony), *fleshy*, or an intermediate combined type. In the dry types, the entire *pericarp* or ovary wall becomes desiccated as the fruit matures. Such fruits may be further subdivided into *dehiscent* and *inindehiscent* types, dependent upon whether they do or do not open at maturity.

In the completely fleshy types, the entire pericarp, together with accessory structures in special cases, becomes succulent. In the intermediate *dry-fleshy* forms, part of the pericarp becomes desiccated; or, in some cases, hardened; while other regions of the ovary wall may remain fleshy. In such types (drupe) the pericarp consists of an outer fleshy portion or *exocarp* and the *endocarp*, which forms a stony pith. These categories may be further subdivided on the basis of the number of carpels and accessory structures involved in the development of the fruit. (Table II.)

DRY FRUITS. — The principal *inindehiscent* dry fruits are the *caryopsis* or *grain*, the *akene*, the *schizocarp*, and the *nut*. The *caryopsis* develops from a single carpel and contains a single seed. In its development, the integuments may be partially disorganized and the remainder of the seed coat becomes so closely appressed to the pericarp that the two structures cannot be readily separated in the mature grain. The *akene* may be the product of the development of one or two carpels, the former being the case in the Ranunculaceae, and the latter obtaining in the Compositae, in which the receptacle is also a part of the fruit. (Fig. 39, A, B.) The fruit is one-seeded, differing from the *caryopsis* in that the pericarp can be removed from the mature seed.

TABLE II
CLASSIFICATION OF FRUITS

CLASSIFICATION OF FRUITS	STRUCTURE			
	One Carpel	Two or More Carpels	Two or More Carpels Plus Stem Axis	Carpels Plus Stem Axis and Accessory Parts
DRY Indehiscent	CARYOPSIS (GRAIN) Gramineae (<i>Zea</i>) AKENE Ranunculaceae (<i>Ranunculus</i>)	AKENE Compositae (<i>Lactuca</i>) SCHIZOCARP Umbelliferae (<i>Apium</i>) SILIQUE Cruciferae (<i>Raphanus</i>)		
DRY Dehiscent	FOLLICLE Ranunculaceae (<i>Delphinium</i>) LEGUME Leguminosae (<i>Pisum</i>)	CAPSULE Malvaceae (<i>Gossypium</i>) Liliaceae (<i>Allium</i>) SILIQUE Cruciferae (<i>Brassica</i>)	CAPSULE Iridaceae (<i>Iris</i>)	
DRY-FLESHY	DRUPE Rosaceae (<i>Prunus</i>)	DRUPACEOUS BERRY AQUIFOLIACEAE (<i>Ilex</i>)	POME Rosaceae (<i>Pyrus</i>) AGGREGATE Rosaceae (<i>Fragaria</i> and <i>Rubus</i>)	MULTIPLE Moraceae (<i>Ficus</i> — Fig) (<i>Morus</i> — Mulberry) Bromeliaceae (<i>Ananas</i> — Pineapple)
FLESHY	BERRY Berberidaceae (<i>Podophyllum</i>)	BERRY Solanaceae (<i>Lycopersicum</i>) Rutaceae (<i>Citrus</i>)	PEPO (INFERIOR BERRY) Cucurbitaceae (<i>Cucurbita</i>)	

The *schizocarp* consists of two or more carpels, each of which is an indehiscent *mericarp* containing a single seed. At maturity, the

mericarps split apart, each one resembling an akene in general structure. This type is characteristic of the Umbelliferae and is also found in the Geraniaceae. Where the mericarp is winged (maple), the mericarp is called a *samara* or *key*. In the *nut*, the structure resembles an akene, but the dry pericarp becomes thick and hard. The term has been loosely applied to many fruits (almond, walnut, cocoanut); seeds (Brazil-nut); and to legumes

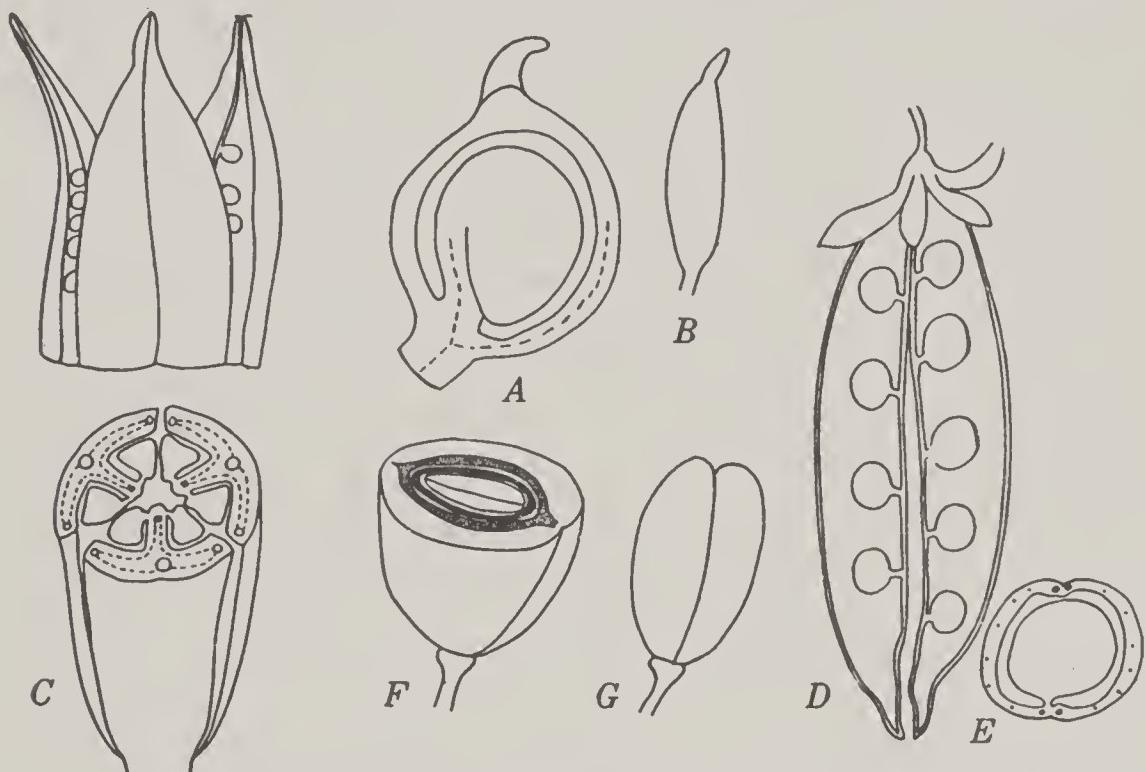


FIG. 39. Fruit types: *A, B*, akene; *C*, capsule of Iris; *D*, pod or legume of pea; *E*, trans-section of same; *F, G*, the drupe, plum.

(peanut); but among the true nuts are the acorn, chestnut, and hazelnut.

The principal *dehiscent* dry fruits are the *follicle*, *legume*, *capsule*, and *siliques*. The follicle and legume fruit are developed from single carpels, and differ from each other primarily in their manner of dehiscence. In the *follicle*, there is a single line of dehiscence which occurs along the suture on its adaxial surface; while, in the *legume*, two sutures are formed and the fruit splits along both at maturity. (Fig. 39, *D, E.*) The *capsule* develops from two or more carpels and may involve a portion of the axis as well (Iris). (Fig. 39, *C.*) The dehiscence in the capsule may be *loculicidal* or *septicidal* or both; and in the poppy, it occurs by means of pores. In the loculicidal type, the lines of dehiscence bisect each carpel longitudinally in the region of the abaxial bundle; in the septicidal type, the lines

of dehiscence correspond to the points of union or non-divergence of the adjacent carpels.

The *silique* is characteristic of the Cruciferae and consists of two carpels which form a bilocular ovary with a longitudinal septum. In most genera, the two valves of the fruit separate longitudinally; but in a few instances (radish) the silique is indehiscent. Where the fruit is short it is sometimes called a *silicle*.

FLESHY FRUITS. — The principal fleshy fruits are the *berry* and the *pepo*. The *berry* develops from the ovary of a hypogynous flower; and produces a fleshy pericarp as it matures. In most cases, the

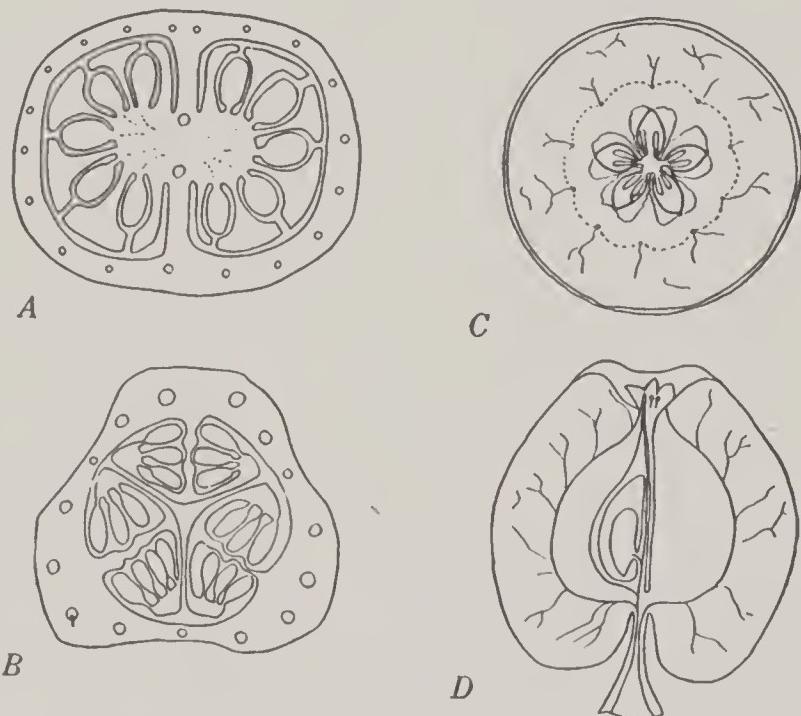


FIG. 40. Fruit types: A, the berry, a bilocular fruit of the tomato; B, pepo, cucumber; C, pome, the apple in transection; D, the same in longisection. (B and C drawn by Kraus.)

berry is derived from two or more carpels (tomato); but it may develop from a single carpel (*Podophyllum*, May apple). (Fig. 40, A.) The citrus fruit is also a berry of a specialized type, sometimes called a *hesperidium*, in which the dorsal walls of the carpels develop into a thick rind and the central portion of the fruit involves the axis as well as the carpels.

In the *pepo*, or *inferior berry*, the fruit develops from an epigynous flower in which the tissue of the non-diverged receptacle surrounds the pericarp and forms an outer rind which in squashes and pumpkins may be very hard. The edible portion consists of the carpillary walls, often mainly the placentae; and the enveloping receptacle. (Fig. 40, B.)

DRY-FLESHY FRUITS. — Several of the major fruit types are in part dry and in part fleshy. In this intermediate group are the *drupe*, *pome*, *aggregate*, and *multiple* types. The *drupe* or *stone fruit* develops from a single carpel in which the pericarp is differentiated into a thin *epicarp* or skin of the fruit, a fleshy *mesocarp*, and an *endocarp* which is hard and stony (plum, apricot, peach). (Fig. 39, F, G.) The mature fruit commonly contains a single seed, but two ovules generally arise, one of them aborting as the fruit develops. The term *drupe* in a less restricted sense is also applied to the fruits of some members of the Caprifoliaceae (elder, Viburnum) which are tricarpellate and may have one to three seeds.

In the *pome* (apple) the fleshy outer portion is formed by the undiverged floral parts which surround the ovary, together with the carpels in whole or in part. The pericarp consists of a papery endocarp forming the inner limit of the core, and a fleshy mesocarp and exocarp. (Fig. 40, C, D.) The *aggregate* fruit is composed of several simple fruits developed from a flower having several simple pistils. In some instances, the axis does not comprise a part of the edible structure. The raspberry represents a form in which the receptacle is readily separated from the small edible drupes; while, in the blackberry, it is not. In the strawberry, the edible tissue is the fleshy receptacle on which a large number of small akenes are borne.

The *multiple* fruit differs from the aggregate in that it is the product of the conjoint development of several flowers, rather than being derived from several pistils of a single flower. While the multiple types resemble one another in this principle of organization, they may be quite variable with respect to the manner of differentiation and the number of accessory parts that enter into the fruit structure. In the fig, the fleshy receptacle is a hollow chamber on the inner surface of which the flowers are borne. The flower cluster may contain both staminate and carpellate flowers or these may occur in separate inflorescences. This type of multiple fruit is sometimes called a *synconium*. In the mulberry, the staminate and carpellate flowers develop in separate inflorescences; and, in the latter, each flower develops a fruit which is nut-like and surrounded by a fleshy pericarp. As the fruits develop, they become closely aggregated; and, together with the fleshy receptacle or axis, form a multiple fruit or *pseudocarp*.

A third multiple type is the pineapple, *Ananas*, in which the flowers are also borne in dense heads that are crowned by a tuft of

leaves. The fruit involves the entire inflorescence, and individual fruits, which are pomaceous and fleshy throughout, are surrounded by a fleshy mass developed from the bracts, sepals, petals, and axis of the inflorescence. A somewhat different multiple type occurs in the globe artichoke, *Cynara*, in which the axis terminates in a globular head that is surrounded by numerous involucral bracts. The heads, together with the bracts, are harvested when immature; and the bases of the involucral leaves and the apex of the inflorescence constitute the edible portion.

THE SEED. — In angiosperms, the *seed* consists of an *embryo* or embryos surrounded by a covering which is generally *integumentary*. *Endosperm* and *nucellar* tissue containing reserve foods may be present; but, frequently, one or both of these tissues are lacking, in which case the food reserves are stored in the cotyledons.

Following pollination, fertilization is effected by the union of one of the two microgametes and the megagamete. The resultant zygote undergoes divisions which initiate the embryo sporophyte. The development of the endosperm precedes or parallels embryogeny and begins following the union of the second microgamete with the polar nuclei to form the endosperm nucleus. The formation of endosperm tissue may proceed more rapidly than the development of the embryo, and food reserves are accumulated in the endosperm cells. The event of double fertilization probably represents the point at which the seed may be differentiated from the ovule; since, from that time, subsequent developments are concerned directly with the embryogeny of the new sporophyte generation and its related nutritive tissues.

THE EMBRYO. — The *embryo* in angiosperms consists of a *hypocotyledonary axis*, one or two *cotyledons* (infrequently three or more occur), and an *epicotyl*. The degree of epicotyledonary development prior to the germination of the seed is variable. In some cases (*Pisum*, *Zea*), the growing point of the epicotyl may differentiate one or more leaf primordia above the cotyledonary node; while, in others, it may consist of nothing more than a small mass of meristematic cells. The growing point of the hypocotyl may be organized as a well-defined primary root in which the histogens and root cap are definitely determined; or it, too, may consist of nothing more than a rudimentary terminal meristem.

Embryogeny is extremely varied with respect to the details of ontogeny. The descriptions given by Hanstein (8) for *Capsella*,

Schaffner (9) for *Sagittaria*; and Souèges (10) for *Allium*, outline the general sequence of events for dicotyledons and monocotyledons respectively; but the details should be described for each plant individually.

In the dicotyledonous embryogeny, the zygote usually divides transversely to form an *apical* and *basal* cell; and subsequent transverse divisions, which may involve the apical cell or both daughter cells, result in the formation of a *proembryo* consisting of a filament of cells of varying length. In most cases, the derivatives of the apical cell of the proembryo form the *embryo*; while the basal cell or its derivatives and the remaining linear cells of the proembryo form the *suspensor*. The first division of the apical cell of the proembryo is usually longitudinal. This is followed by a second division in the longitudinal plane, at right angles to the first division, and a transverse division, or the order may be reversed. In either case, the octant stage is reached and the transverse division delimits the cotyledonary from the hypocotyledonary portion of the embryo.

Following the octant stage, the histogens may be differentiated, and the dermatogen is cut off by periclinal divisions which occur first in the terminal portion of the embryo and progress toward the hypocotyledonary region. The differentiation is continued rapidly so that the dermatogen is soon complete except at the apex of the primary root which is in contact with the adjacent cell of the suspensor. This portion of the dermatogen is usually derived from the uppermost cell of the suspensor, and the periblem and plerome then differentiate within the dermatogen. The epicotyl and cotyledons are derived from the four apical octants of the young embryo, while the major portion of the hypocotyl is derived from the four basal ones. The embryo rapidly develops its hypocotyledonary axis and cotyledons, the degree of differentiation which it may attain being determined largely on the basis of the speed with which the fruit and seed ripen.

In a monocotyledonous embryogeny, as represented by *Allium*, the first division of the zygote is transverse, producing an apical and basal cell. This is followed by a second transverse division of the basal cell so that a three-celled embryo is formed. The subsequent divisions of the apical cell do not appear to be entirely regular; but, as a result of oblique or vertical divisions of the apical cell, quadrants of the embryo are formed which produce the cotyledon

and growing point of the epicotyl. Subsequent divisions of the intermediate cell produce the hypocotyledonary portions of the axis as well as the root cap, and the inferior cell of the linear triad gives rise to the suspensor by a series of divisions. As the hypocotyl develops, there is a blocking off of a clearly defined plerome, periblème, dermatogen, and root cap.

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PART II. ECONOMIC PLANTS

CHAPTER V

GRAMINEAE

ZEA MAYS

THE grass family includes many important crop plants which are used for forage and as cereals. Among the cereals grown in the United States are: oats, *Avena sativa* L.; barley, *Hordeum vulgare* L.; rye, *Secale cereale* L.; rice, *Oryza sativa* L.; wheat, *Triticum* sp.; and corn, *Zea Mays* L. Sugar cane, *Saccharum officinarum* L., is also an outstanding economic grass; and there are numerous meadow and range grasses which constitute the chief forage crops.

GENERAL MORPHOLOGY

THE ROOT. — Corn is an herbaceous monocotyledon with an annual cycle. The mature plant has an extensive fibrous root system consisting of several whorls of adventitious roots some of which become wide-spread laterals, others deeply penetrating vertical roots. Weaver (24) reports,

"A lateral spread of 3.5 feet on all sides of the plant is not uncommon even early in its development, and a depth of penetration of 5 to 6 feet is usual. The degree of spreading as well as the depth varies somewhat with soil and other conditions, the root system probably reaching its greatest development in deep mellow soils only moderately well supplied with water." (Fig. 41.)

The primary root may persist during the entire life of the plant, although it frequently decays; but it has little functional importance after the establishment of the adventitious root system.

THE SHOOT. — The stem of the corn plant varies within a wide range, some of the dwarf varieties being less than 2 feet tall while certain types of field corn may attain a height of 12 to 15 or even 20 feet. Northern varieties usually reach a height of 6 to 7 feet,

while the southern ones frequently attain the maximum noted above. The main stem axis is sometimes unbranched, except for lateral carpellate inflorescences or "ears" which are borne on short branches; but tillers, suckers, or lateral branches may arise from buds located in the axils of the lower leaves. The latter occasionally develop as ears or they may form vegetative stems which in turn develop adventitious roots and produce inflorescences.

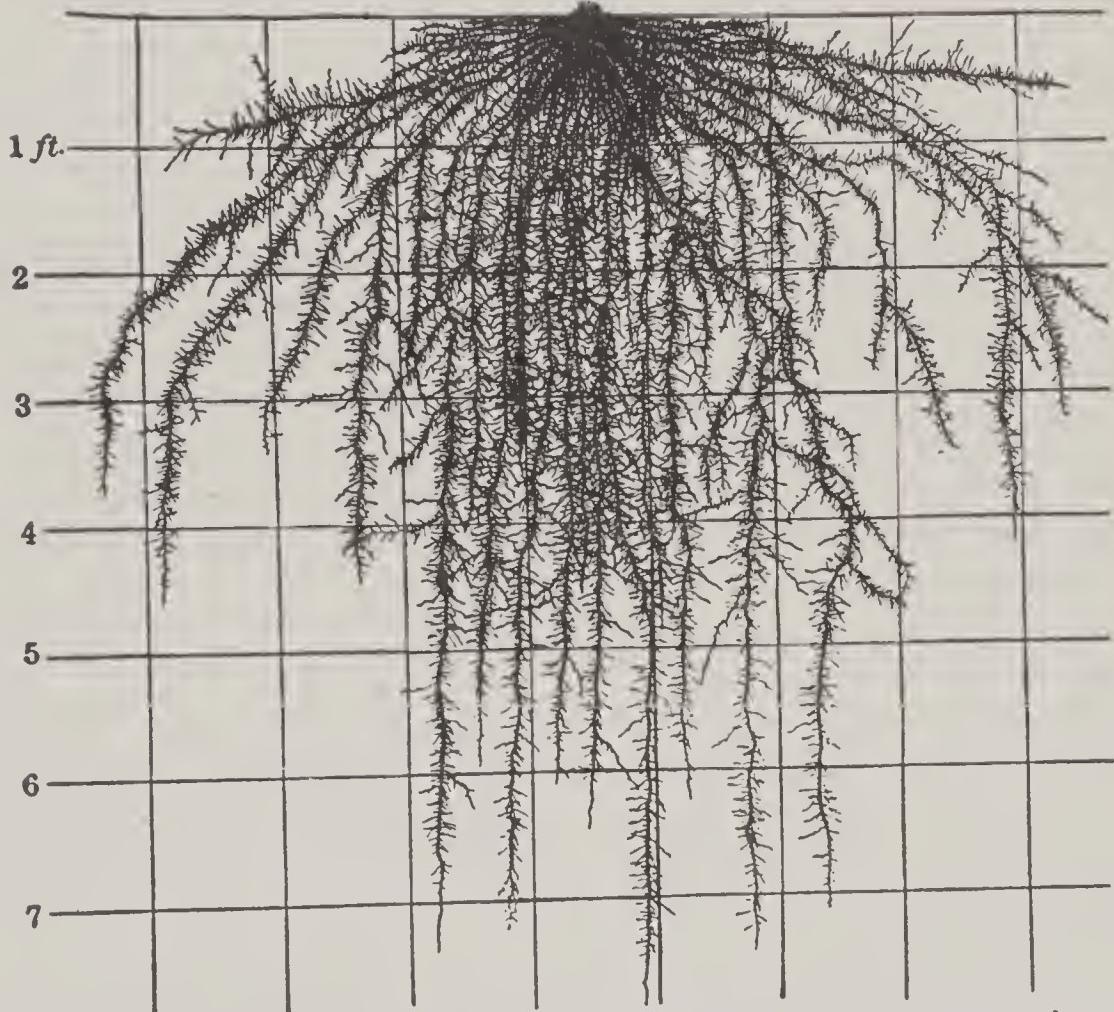


FIG. 41. The mature root system of corn showing its lateral and vertical spread.
(After Weaver, *Root Development of Field Crops*, McGraw-Hill Book Co.)

The stem is solid with the characteristic jointed appearance of all grasses, and the internodes are alternately furrowed just above the node on the side next to the leaf blade. This furrowing is related to the formation of axillary buds, and, consequently, is more pronounced in the internodes above each ear than in the upper internodes where the buds are not well developed.

The leaves are alternate and two-ranked as in other grasses. Each leaf, except the scutellum and coleoptile, consists of a basal sheath, ligule, and blade. The sheath surrounds the internode.

for some distance above the node from which it arises and its edges overlap on the side of the axis distal to the blade. According to Weatherwax (22), the collar-like ligule develops from the adaxial epidermis at the top of the sheath, fitting tightly around the stem and the blades or sheaths of the included leaves. The long, flat blade is auricled at the base and is somewhat fluted or wavy along its edges at maturity. This results from inequalities in the growth rate of the marginal and central cells of the leaf. There is a prominent midrib with many smaller, parallel veins which do not anastomose with one another directly, but may be cross-connected at frequent intervals by transverse veinlets. The number of leaves on a given axis is variable, ranging from 10 to 18 or more.

THE INFLORESCENCES. — Corn is monoecious, normally producing staminate and carpellate flowers on separate inflorescences on the same plant. The staminate flowers are borne on a terminal panicle (tassel) consisting of a central spike and several lateral branches or rachises arising from the central spike in a spiral arrangement. The carpellate inflorescence (ear) originates in the axil of one of the lower leaves and is borne on a short branch or shank. Leaves arise from each node of the shank and form the husks of the ear. The internodes of the shank are but slightly elongated, the upper ones being progressively shorter than the lower so that the husks overlap one another closely. In most cases, the leaves which form the husks are only partially developed; but occasionally they may have normal blades and ligules.

Variations in the monoecious condition are not uncommon. Plants may develop which have staminate inflorescences only. In other cases portions of the tassel, usually the central spike, produce carpellate spikelets bearing fruits. Another variation consists in the development of staminate flowers on the ear, usually near its apex; and functionally perfect flowers have been known to occur. In suckers, the inflorescences formed may be normal ears or normal tassels or there may be any of the variations noted above.

ANATOMY

THE MATURE GRAIN. — The fruit of maize is a caryopsis in which the pericarp, remains of the integumentary tissue, and nucellar membrane are so intimately connected at maturity as to appear fused. The mature grain consists of the hull which is made up of the pericarp and remains of the integuments, which may or may not

be present, the nucellar membrane, the aleurone layer, the starchy endosperm, and the embryo. The pericarp has been described by Winton (25), Randolph (15), and others. It has several layers, the outer zone or epicarp consisting of elongated cells with thick porous walls and a well-developed cuticle covering the outer surface. The mesocarp or central zone is several layers thick and the cells resemble those of the epicarp, except that the walls are somewhat thicker. Underlying this is the spongy parenchyma, consisting of cells with radiating arms which are joined in such a way as to form relatively large intercellular spaces. This zone is much more pronounced at the pointed end of the grain. Adjacent to the parenchyma is a layer of tube cells. These are the inner epidermal cells of the pericarp which are drawn apart laterally as the grain enlarges and give the appearance of a network over its inner face. Within the pericarp, there may or may not be some remnants of the integuments. The outer integument, which never completely encloses the nucellus, is crushed or resorbed early in development; but, in some cases, portions of the inner integument persist. This integument is two-layered except near the micropyle, where there are three to five layers. Weatherwax (22) found crushed remains of this tissue in the mature grain and referred to it as a testa. Randolph (15) made an ontogenetic study of the grain in the variety *Pride of Michigan* and "concluded that the maize caryopsis has no true seed coat."

The nucellus in the mature grain consists of non-cellular remains of the disintegrated tissue and a suberized membrane lying between the pericarp and the aleurone layer. The endosperm consists of an aleurone layer and the starchy-parenchyma. The thick-walled, cubical, aleurone cells lie directly within the nucellar membrane; and the zone is usually one cell layer in thickness, although it may be two-layered at some points owing to periclinal divisions. The starchy-parenchyma consists of thin-walled storage cells. Those immediately abutting the aleurone layer are smaller than the more centrally located ones which constitute the horny portion of the endosperm. They are higher in protein content than the starchy endosperm and contain large numbers of small polygonal starch grains. In the larger cells of the starchy endosperm, the grains are for the most part rounded, and the larger ones have a distinct hilum. The amount of horny and starchy endosperm varies greatly with the variety of corn, as do the percentages of carbohydrates, pro-

teins, and oils contained in the storage and embryonic tissues of the grain. According to Randolph, the antipodal cells frequently proliferate during the development of the caryopsis, and may persist in the mature grain, forming an oval "mass of haploid tissue between the aleurone layer and the pericarp at the tip of the kernel."

THE EMBRYO. — The embryo lies embedded in the endosperm at one side and toward the base of the caryopsis. (Fig. 42.) Its axis is oriented in such a manner that the primary root is directed toward the attached end of the grain. The scutellum is a large lateral structure lying directly in contact with the endosperm, and its edges partially enclose the embryonic axis. It diverges at the cotyledonary plate or first node of the seedling axis. The tissue of the scutellum consists of parenchymatous cells except for the abaxial surface, which is covered by a layer of epithelial cells where the scutellum is in contact with the endosperm. The occurrence of glands in this

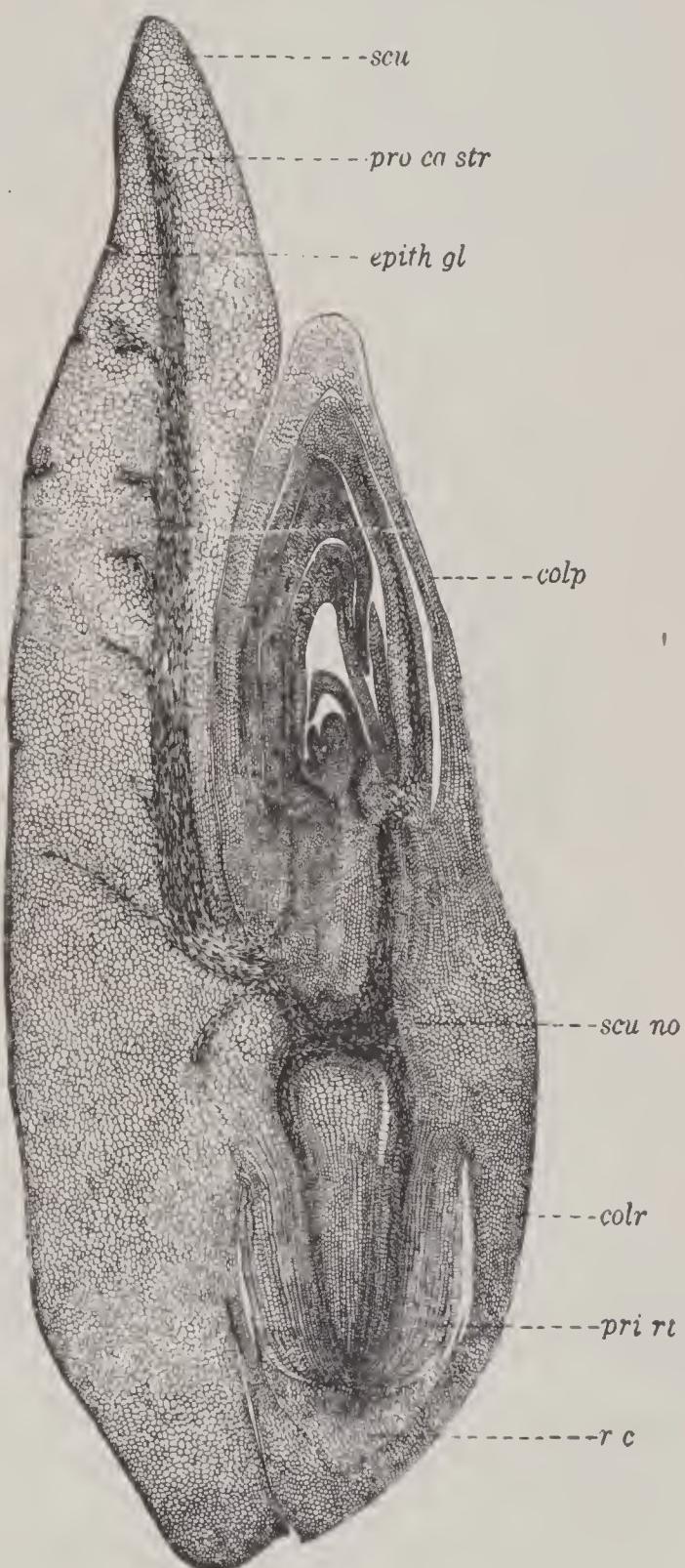


FIG. 42. Longisection of the mature embryo of corn: *colp*, coleoptile; *colr*, coleorhiza; *epith gl*, epithelial gland; *pri rt*, primary root; *pro ca str*, procambial strand; *rc*, root cap; *scu*, scutellum; *scu no*, scutellar node. (After Avery.)

layer has been reported by Sargent and Robertson (17) as follows:

"The glands are scattered over the whole surface of the epithelium except where it covers the top of the scutellum." They "differ greatly in size. Some of the smallest are funnel-shaped pits, others shallow slits, and it is very difficult to draw the line between structures which deserve the name of glands and mere depressions or wrinkles."

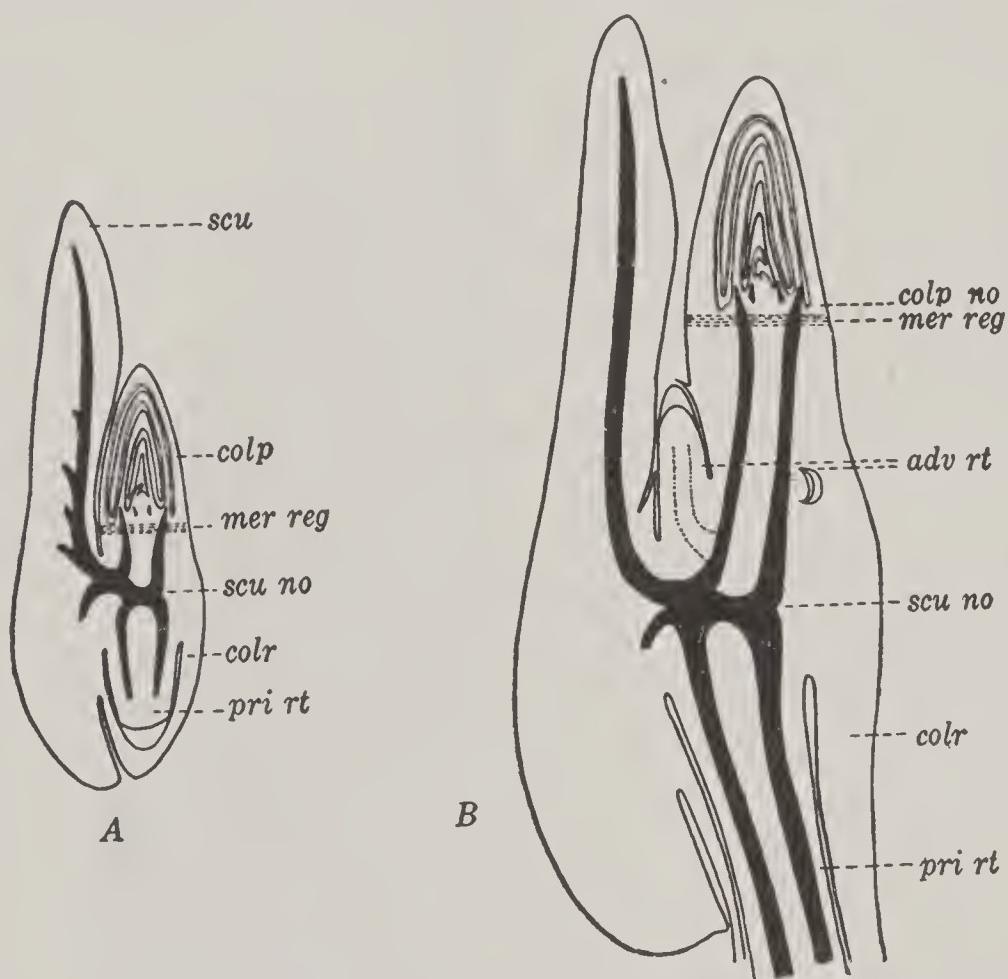


FIG. 43. Longitudinal diagram of the embryo showing vascular system and meristematic regions: A, before germination; B, after germination: *adv rt*, adventitious root; *colp*, coleoptile; *colp no*, coleoptilar node; *colr*, coleorrhiza; *mer reg*, meristematic region; *pri rt*, primary root; *scu*, scutellum; *scu no*, scutellar node. (After Avery.)

Their frequency is variable, but they are more abundant on the upper portion of the abaxial surface and on the wings of the scutellum than on the lower portion.

The primary root is enclosed by the coleorrhiza; and the partially disintegrated suspensor, which persists during the maturation of the grain, may be seen in median longisections at its distal end. The coleoptile is cone-shaped, enclosing the embryonic leaves, of which about five develop, and the growing point of the epicotyl.

It arises at the second node, the internodal region between the scutellar node and the coleoptilar node forming a short, slightly elongated neck in the embryo. (Fig. 43.) The other internodes are unelongated so that the embryonic leaves enclosed by the coleoptile closely surround the leaf primordia and the growing point of the stem axis. Two or more adventitious roots originate just

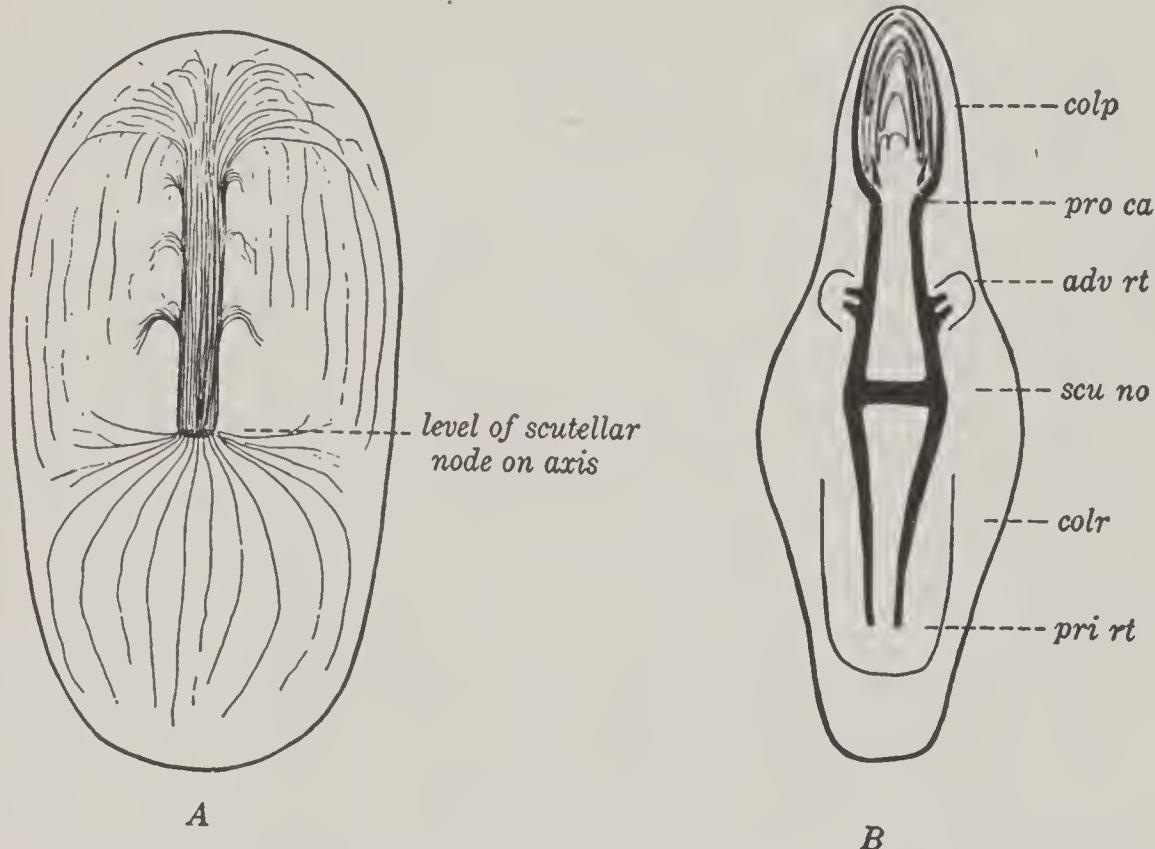


FIG. 44. A, face view diagram of scutellum showing its vascular anatomy; B, face view diagram of the axis of the embryo showing the vascular system: *adv rt*, adventitious root; *colp*, coleoptile; *colr*, coleorhiza; *pri rt*, primary root; *pro ca*, procambial strand; *scu no*, level of scutellar node. (After Avery.)

above the level of the scutellar node and are at first directed laterally upward. (Fig. 44, B.) The primary root has a well-defined root cap; and, in the stelar portion, the differentiation of vascular elements is well advanced.

Avery (1) has described the vascular system of the embryo:

"The embryonic vascular system consists partly of a large procambial strand laid down in the scutellum. This main procambial bundle branches throughout its length. In the lower part of the scutellum are several procambial strands which radiate out and downward from the level where they diverge from the axis. In longitudinal face section they appear much like the ribs of an inverted fan. (Fig. 44, A.) The procambial bundles from the upper and lower ends of the

scutellum are joined at the level of divergence of the scutellum from the axis and within the embryonic axis are connected directly with the stele. Continuing from the place of attachment of the scutellar bundle to the stele it is easily possible to trace procambial elements to the first leaf above the coleoptile. The vascular system of the coleoptile consists usually of two vascular bundles one on either side. They arise directly from the stele on the embryonic axis, at the upper end of the neck-like interval in the axis already referred to."

GERMINATION. — In germination, the grain begins to swell, the coleorhiza grows through the pericarp, and is, in turn, penetrated

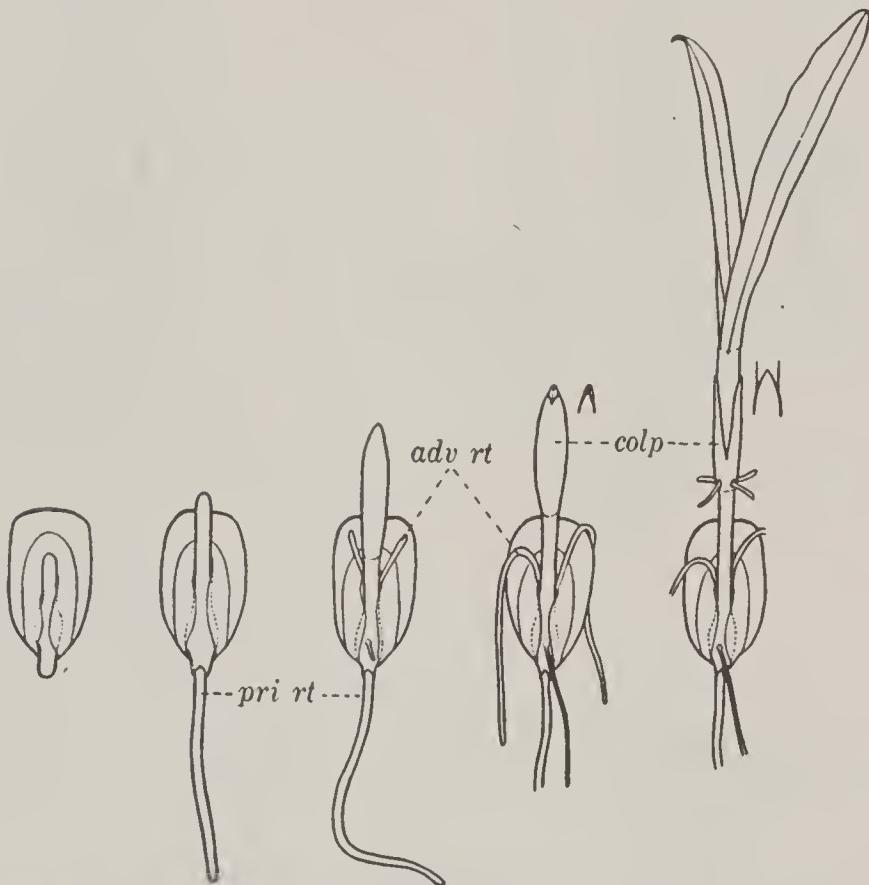


FIG. 45. Stages in the development of the seedling: *adv rt*, adventitious root; *colp*, coleoptile; *pri rt*, primary root. (After Avery.)

by the primary root, which elongates very rapidly. The coleoptile is pushed upward by the elongation of the first internode, which results from the activity of an intercalary meristem located just below the second or coleoptilar node. This internode differs in this respect from the internodes above it; since, in all others, the intercalary meristems are located near the base. When the coleoptile has been raised until its base reaches the soil surface, its edges spread apart at the tip and the enclosed foliage leaves begin to emerge. The adventitious roots, arising above the cotyledonary

node, grow upward until they emerge through the pericarp and they then incline downward. Later a whorl of adventitious roots, four or more in number, originates just above the level of the second node. (Fig. 45.)

THE SEEDLING AXIS. — The seedling axis has been variously interpreted by anatomists working with the grasses. Celakovsky (4) considered the scutellum as homologous with the blade of a leaf and the coleoptile as comparable to the closed ligule of the foliage leaf of the grasses. He regarded the portion of the axis between the scutellum and the coleoptile as an elongated node and called it the mesocotyl. Worsdell (26) agreed in part with Celakovsky and considered the mesocotyl an elongated primary node. He interpreted the scutellum as the lamina of the cotyledon, and the coleoptile as being a part of the cotyledon comparable to the ligule of a foliage leaf. He also stated that "the position of the cotyledon in all monocotyledons as shown by the facts of development, there being no epicotyledonary axis present on its first formation, is always terminal, and is the natural continuation and termination of the hypocotyl." Sargent and Arber (16) regarded the scutellum as the sucking apex of the cotyledon, the coleoptile as the cotyledonary sheath, and the mesocotyl as a unique structure representing a fusion of the cotyledonary stalk with the hypocotyl. Weatherwax (21) pointed out that the embryogeny of maize indicates "that the coleoptile is the homologue of a foliage leaf and that the cotyledon is a lateral organ." Avery (1) stated that the scutellum is the cotyledon, "the coleoptile is homologous with a foliage leaf and is the second leaf of the plant. . . . The elongated structure between the cotyledon and the coleoptile is the first internode of the axis." This interpretation appears to be in accord with the anatomy of the corn seedling; and, under it, the use of the term *mesocotyl* is without point.

THE PRIMARY ROOT. — The mature primary root has an exarch, radial siphonostele with a central pith composed of large parenchymatous cells. In the embryonic axis, three distinct histogens are differentiated in the meristematic growing point of the primary root. (Fig. 46.) The plerome, or innermost of these histogens, produces the tissues of the stele and included pith. The periblemdermatogen consists of a single layer of meristematic cells overlying the plerome. Periclinal divisions of the lateral cells of this histogen produce two daughter cells, the outer daughter cell becoming

an epidermal initial and the inner one a cortical initial. Subsequent anticlinal divisions of the epidermal initials produce the epidermis of the root, while divisions of the cortical initials in all three planes result in the formation of several parenchymatous layers of the cortex. The calyptrogen lies immediately outside the

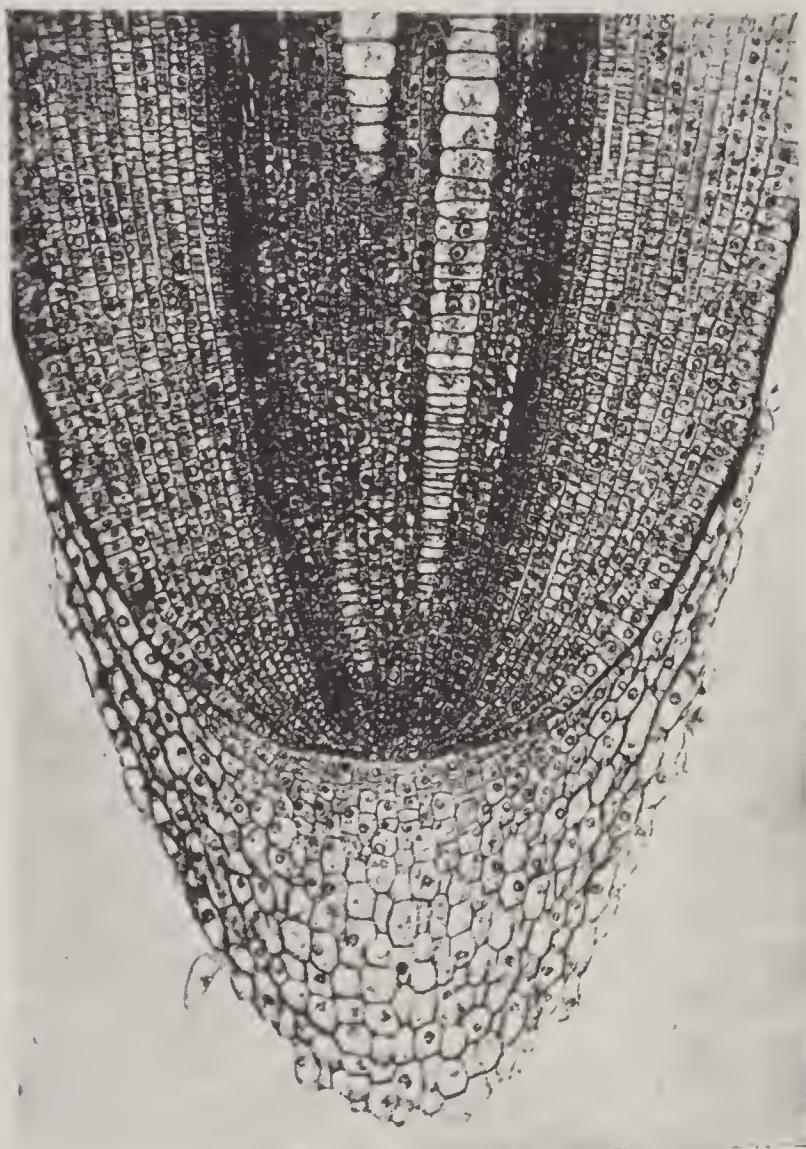


FIG. 46. Median longisection through the tip of the primary root of corn showing the histogens. (See also Fig. 15.)

periblem-dermatogen layer and by successive periclinal divisions produces the multi-layered root cap. Some anticlinal divisions of root cap cells may follow the initial periclinal divisions.

In the development of the stelar tissue, the protoxylem is differentiated early in ontogeny, consisting of slender elongated elements with spiral or annular thickenings. The vessel segments of the metaxylem increase in diameter very rapidly and may be broader than they are long, but final maturation is not completed

until after that of the protoxylem. As they mature, the vessel segments become somewhat longer, the end walls are resorbed, and the secondary thickening of the lateral walls results in a narrowly reticulate or pitted type. The phloem elements are elongated and thin-walled.

The number of protoxylem points is variable, ranging from 20 to 40, and there are commonly two or three protoxylem strands to each large metaxylem vessel.

(Fig. 47.) The groups of primary phloem are on radii alternate with the protoxylem and abut the pericycle. The parenchymatous cells which lie between the xylem points and surround the phloem become thickened and lignified, forming a continuous zone of thick-walled connective tissue as the root matures. The pericycle consists of a single layer of thin-walled cells which may become thick-walled later in ontogeny; and lateral roots originate in this region. The endodermis is also a single layer; and, at maturity, its cells have the U-shaped type of thickening in which the end, radial, and inner tangential walls are reinforced. The passage cells have no secondary thickening except the Caspary strip, and they usually occur on the same radii as the protoxylem points. (Fig. 14.) The cortex is comprised of several layers of parenchymatous cells bounded externally by a more or less ephemeral epidermis. It produces an abundance of root hairs immediately back of the zone of root elongation; but disintegrates later, and the outer cells of the cortex form a lignified and suberized exodermis.

The ontogeny of the seminal roots arising above the scutellar node, and of the adventitious roots that develop later in the basal intercalary meristems of higher internodes, is essentially like that

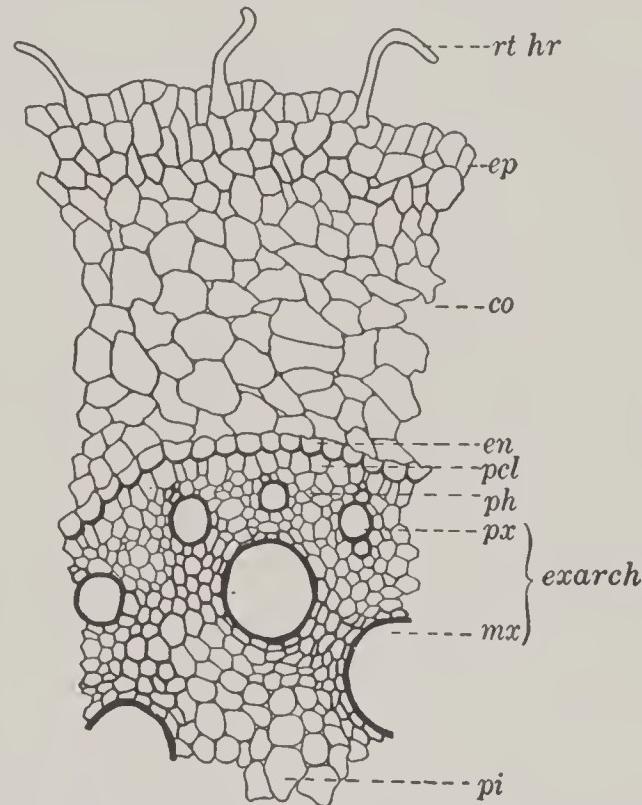


FIG. 47. Transection of a sector of the primary root: *co*, cortex; *en*, endodermis; *ep*, epidermis; *mx*, metaxylem; *pcl*, pericycle; *ph*, phloem; *pi*, pith; *px*, protoxylem; *rt hr*, root hair. (After Avery.)

of the primary root. The seminal roots may be somewhat smaller than the primary root with fewer protoxylem points. The principal adventitious or prop roots are much larger than the primary root, and the number of xylem points may be double that found in the primary stele. Another difference exists in the aerial portions of the adventitious roots where the epidermis instead of disintegrating is persistent, developing a cuticle similar to that of the stem.

Adventitious roots may arise in the pericyclic region of the first internode and in the meristematic basal portions of any of the higher internodes. A root primordium is differentiated from a ring of meristematic tissue which is comparable in function and location to a pericyclic zone although there is no definite endodermis to determine its outer limit. The elongating root then forces its way through the cortex and the basal portion of the leaf which ensheathes the node. The emergence of the lateral is accomplished by a splitting of the cells of the regions penetrated and by digestive action. (Fig. 21.)

HYPOCOTYL AND STEM. — The hypocotyl is very limited in extent and strictly root-like in structure so that the description given for the mature primary root applies to the axis up to the cotyledonary node. The vascular transition is epicotyledonary, occurring chiefly in the vascular plate of the first node and in the first internode. It is continued to some degree in the second internode in which transition bundles may be found; and, occasionally, there may be some transitional structures in the third and fourth internodes.

THE FIRST INTERNODE. — The first internode has a central pith with an annular zone of vascular elements bounded by a pericycle and endodermis, both of which are one cell layer in thickness. (Fig. 48.) The cortex, consisting of thin-walled parenchyma, is several cells in thickness and the epidermal cells have a thin cuticle. In the stelar region, there are groups of exarch xylem which usually alternate with endarch collateral bundles. The primary phloem is in a collateral position with respect to the endarch primary xylem; and in an alternate, radial position in relation to the exarch xylem groups. Thus, the transitional region exhibits an intermixture of root-like and stem-like orientations of the vascular tissues.

THE COLEOPTILE. — The coleoptile is the second leaf of the seedling axis and arises at the second node. Its elevation to approximating

mately the soil level is accomplished by the activity of meristematic cells immediately below the second node. (Fig. 49.) The primordium of the coleoptile is initiated as an open sheath; but, as growth continues, the edges soon unite, forming a closed structure although the line of union remains visible, especially near the top.

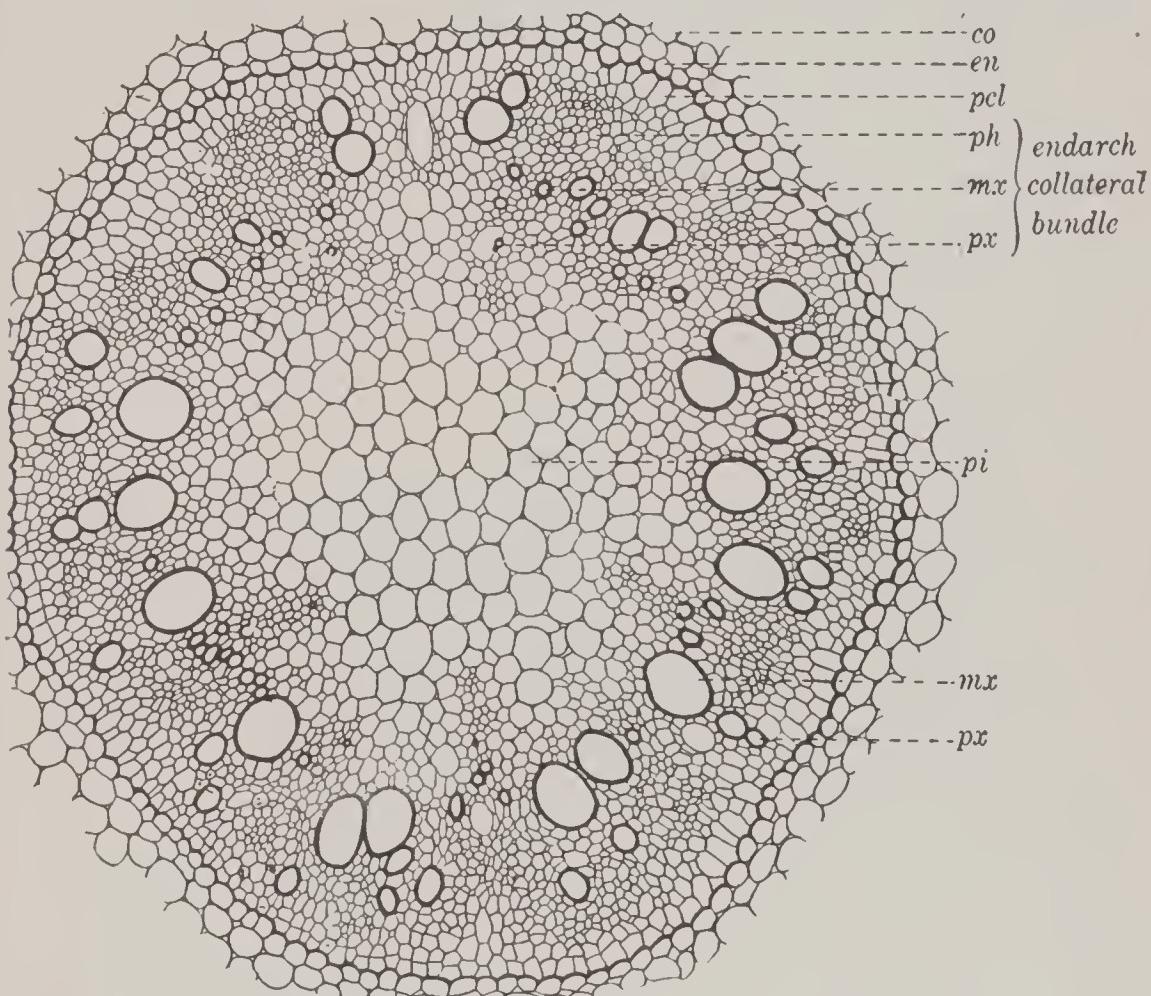


FIG. 48. Transection of the first internode of the axis showing transitional character with endarch collateral bundles, and radial arrangement of primary phloem and exarch xylem: *co*, cortex; *en*, endodermis; *mx*, metaxylem; *pcl*, pericycle; *ph*, phloem; *pi*, pith; *px*, protoxylem. (After Avery.)

The structure of the coleoptile is simple, consisting of a relatively compact chlorenchyma and two vascular bundles which are bilaterally placed. Each bundle is made up of several xylem strands which partially surround the phloem so that it may be regarded as half-amphivasal. In exceptional cases, the number of vascular bundles in the coleoptile may exceed two; and, in some instances, four are formed by a division of the original bundles. Avery (1) has reported "the presence of as many as five bundles. The extra bundles have ordinarily an origin similar to that of the usual two, although in the case of five, the fifth bundle usually arises *de novo*

in the cortex below the coleoptilar node." A bud is seldom differentiated in the axil of the coleoptile. Stomata are found only in the outer epidermis and usually occur in rows on either side of the vascular bundles.

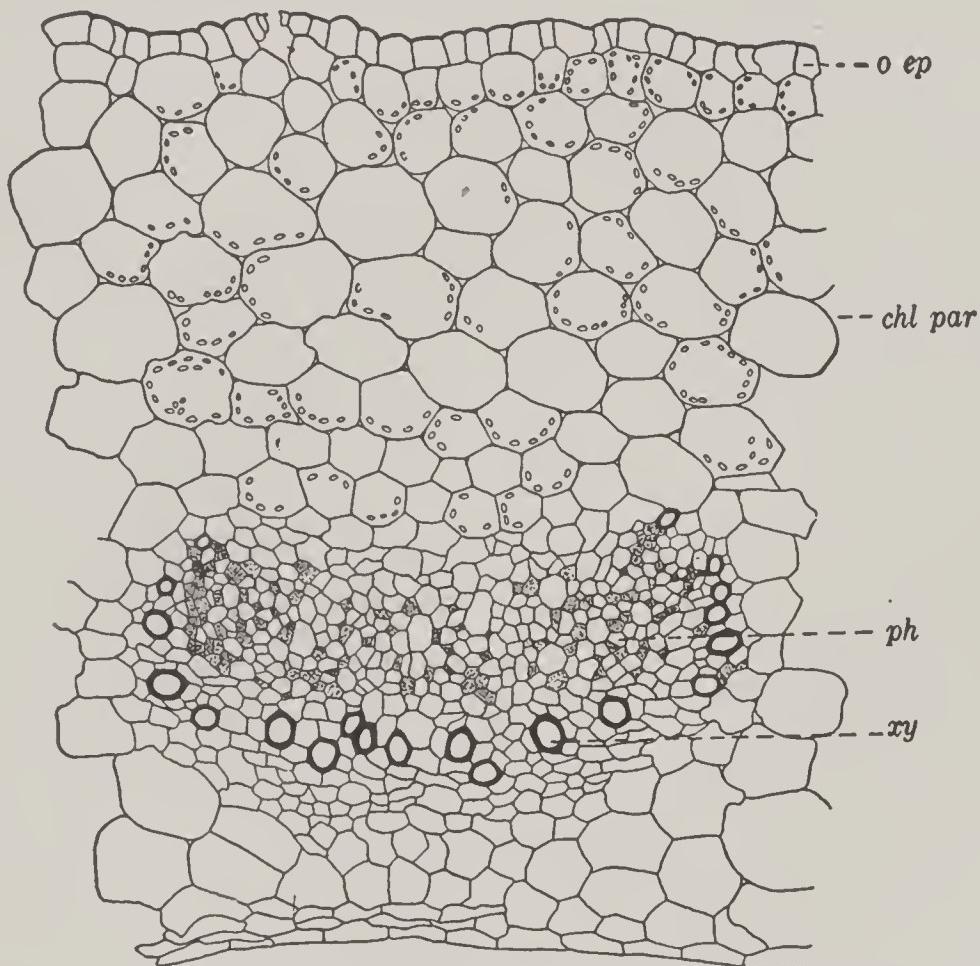


FIG. 49. Transection of a portion of the coleoptile showing coleoptilar bundle: *chl par*, chlorophyll parenchyma; *o ep*, outer epidermis; *ph*, phloem; *xy*, xylem. (After Avery.)

SECOND INTERNODE. — The second internode is also transitional. (Fig. 50.) It is less root-like than the first internode, but lacks the definite meristelic structure of the higher internodes. The cortex is relatively thick, and centrad to it there is a meristematic zone of tissue which is probably of pericyclic origin. In this internode there are transitional bundles of several types, as well as scattered groups of xylem and phloem elements in various orientations. The transition is practically complete at the third node, and the internodes above this point have a meristele of collateral bundles.

Early in ontogeny, the final pattern of the plant is determined. By the time the stem axis is an inch long or even less, all the plant structures — leaves, nodes and internodes, terminal tassel, lateral

ears, primary and adventitious root systems — have been sufficiently differentiated that their topography can be readily determined.

THE STEM. — The mature stem is a meristele with bundles scattered throughout the fundamental parenchyma. The bundles near the periphery of the stem are smaller and more numerous than those

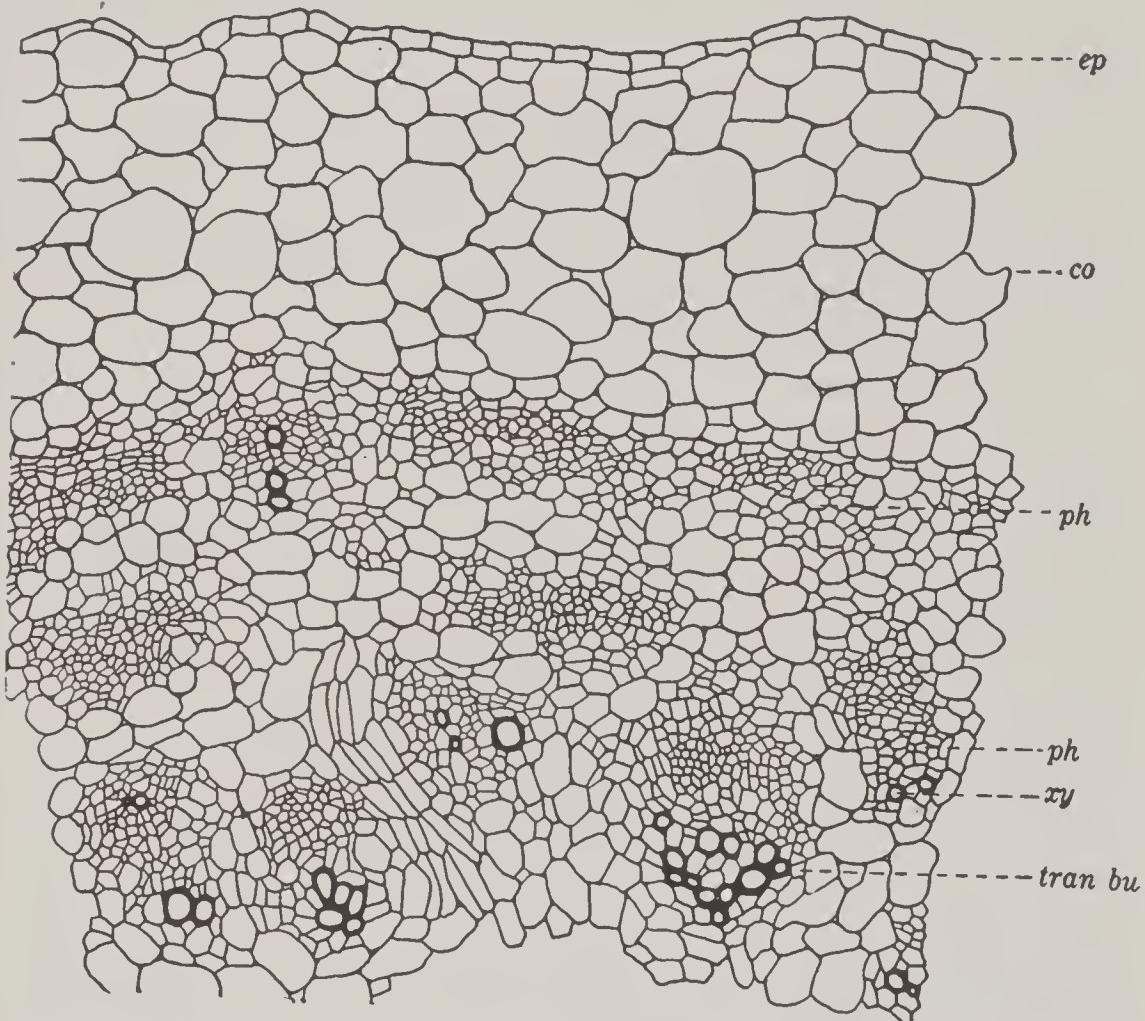


FIG. 50. Transection of the second internode showing transitional character: *co*, cortex; *ep*, epidermis; *ph*, phloem; *tran bu*, transition bundle; *xy*, xylem. (After Avery.)

toward the center of the axis. The centrally located parenchymatous cells are large and thin-walled, with intercellular spaces at their angles. Those adjacent to the epidermis are smaller; and, in the mature stem, become thick-walled and lignified, forming a protective rind inside the epidermis which also lignifies at maturity. The stomata, guard cells, and accessory cells are similar to those of the leaf. (Fig. 25.)

The node is woody and rigid and its vascular anatomy is very intricate owing to the fact that at each node there is a large number

of bundles entering the stem which penetrate the nodal zone horizontally for various distances before they incline downward. In addition to this, although many of the bundles of the internode above pass directly through the node, a certain proportion of them terminate at each node by anastomosing with other bundles.

Evans (6) investigated the vascular anatomy of the node using a technique involving staining with methylene blue and retting. He found that the vascular bundles "seldom pass through more than two or three nodes without branching"; and points out that the nodal complex results from numerous small branches that arise from the vascular bundles as they enter the node, and from the small peripheral bundles. The division, subdivision, and anastomosing of these bundles account for the vascular meshwork which constitutes the nodal plate.

THE STEM BUNDLE. — The collateral or amphivasal bundle is enclosed by a sheath of mechanical tissue, and is generally oriented with the phloem toward the periphery of the stem. (Fig. 51.) There are usually two protoxylem vessels in each bundle, one with annular and the other with spiral wall thickenings. The two large laterally placed metaxylem vessels are either narrowly reticulate or pitted, the pits being of the simple unbordered type. Between the two large metaxylem vessels is a connecting band of smaller pitted tracheids. As the bundle matures, the parenchyma surrounding the two protoxylem elements becomes separated from them, forming an air space or lacuna; and at this time the unthickened portion of the wall of the annular vessel is frequently crushed or destroyed. The phloem, which lies in a collateral position with respect to the xylem, consists of a small number of protophloem cells and metaphloem in which the sieve tubes and companion cells are very regularly arranged. As the bundle matures, the protophloem becomes non-functional and the crushed cells form a narrow band just outside of the metaphloem. The bundle is of the closed type and all the cells of the provascular strand become mature primary vascular elements without the formation of a cambium.

VASCULAR ANATOMY OF STEM. — All the bundles of the stem are common and their downward course is nearly vertical, although there may be some lateral and tangential curvature. The course of the bundles has been described by de Bary (2) following the classic account of von Mohl. The bundles of the leaf trace enter the nodal plate from the base of the leaf and pass downward

through the internode. Upon entering the node, some pass directly downward near the periphery of the stem and are almost radially perpendicular; while others penetrate the stem more deeply, following a horizontal course. These may at first even incline slightly upward and then curve downward toward the periphery, where they become almost vertical. All of the bundles descend through two or three or more internodes without branching or anastomosing with other bundles.

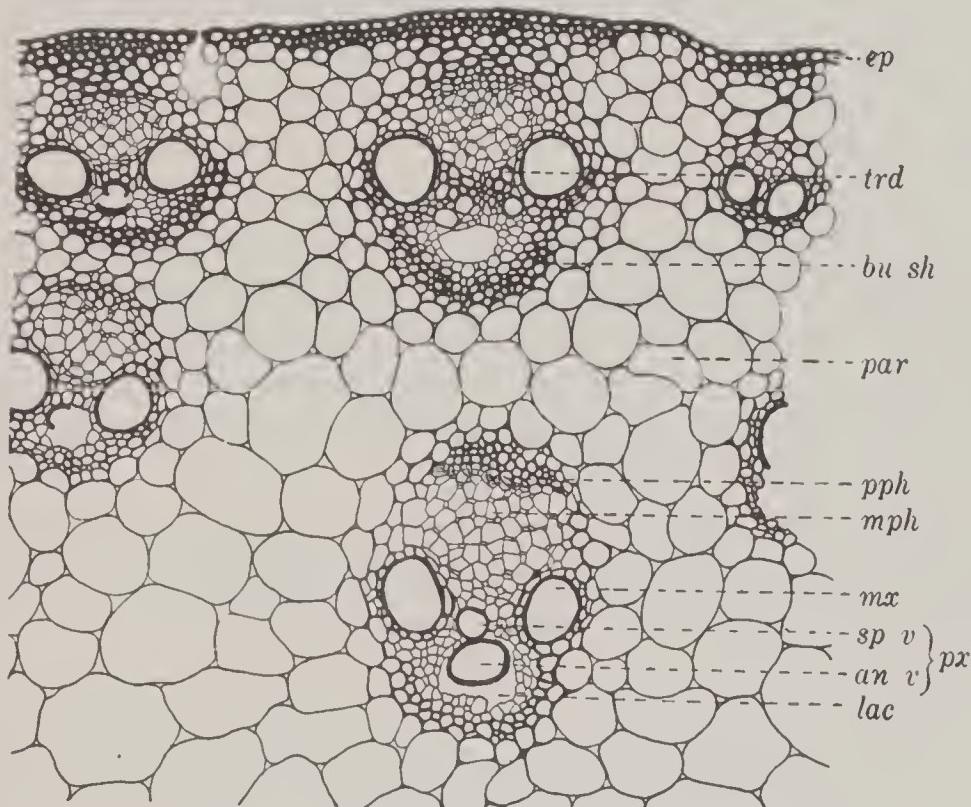


FIG. 51. Section of the sixth internode of the stem: *an v*, annular vessel; *bu sh*, bundle sheath; *ep*, epidermis; *lac*, lacuna; *mph*, metaphloem; *mx*, metaxylem; *par*, parenchyma; *pph*, protophloem; *px*, protoxylem; *sp v*, spiral vessel; *trd*, tracheids. (After Avery.)

As a result of the anastomoses of descending bundles with those which enter the stem at lower nodes, the total number of bundles in the lower internodes is approximately the same. Hershey and Martin (9) investigated the development of the bundles in yellow dent corn and found that 90 per cent of them were differentiated in the lower internodes by the forty-fifth day. The number formed at maturity was 680 for the first internode and 750 for the second.

Since the entering bundles incline toward the periphery of the stem in their downward course, they are more crowded near the surface than in the central portion of the axis. (Fig. 25.) The inclination of the bundles toward the periphery is not readily detected

in mature stems, since the internodes are very long and the outward curvature of the bundles occurs in the internodes prior to internodal elongation by intercalary growth.

THE LEAF. — The leaf consists of a sheath, a collar-like ligule, and a blade. All the main veins are parallel and there are cross-connecting veinlets. The mesophyll is comprised of relatively compact chlorenchyma with few intercellular spaces, and there is no differentiation into palisade and spongy tissue. The collateral vascular bundles are of two sizes, the larger type resembling the stem bundle except in two respects. The mechanical tissue, instead of completely surrounding the bundle, consists of a zone of thick-walled elements, above and below it. This tissue abuts the upper and lower epidermis and, with the mechanical elements of the mid-rib, serves as the chief support of the leaf. Surrounding the bundle is a sheath of chlorophyllose cells in which the chloroplasts are definitely larger than those found in the mesophyll. The smaller type of leaf bundle has no adjacent mechanical tissue and consists of a few xylem and phloem elements surrounded by a sheath of parenchymatous cells containing large chloroplasts. The transverse bundles which cross-connect the small parallel veins with one another or with a larger bundle consist of one or a few xylem elements with or without accompanying phloem elements. (Fig. 52.)

Randolph (14) investigated the cytology of the several types of chloroplasts in corn and found them to be the same in their initial structure. They originate as very minute proplastids and gradually enlarge, developing chlorophyll until they reach maturity. He also observed that both partially developed and fully matured plastids may divide, but was unable to determine the origin of the proplastid because of its small size. The question as to whether the plastids are permanent cell organs with an unbroken genetic continuity or arise *de novo* is still undetermined.

Both epidermal surfaces are cutinized, the lower being more so than the upper; and both contain stomata arranged in parallel longitudinal rows. Varying stomatal counts have been made on maize, but all are in agreement that the number in the lower surface exceeds that in the upper. Moore (12) has made a study of the histology of the upper epidermis and has recognized three zones that run lengthwise of the leaf. These are the zone of bulliform or motor cells, the zone of narrow epidermal cells, and the stomatal

zone. The bulliform zone is a band of epidermal cells two to five or six rows in width which consists of motor cells, basal cells, and the trichomes arising from the latter. The bulliform cells are approximately hexagonal, protruding slightly above the surface of the leaf, and extending deeper in the mesophyll than do the other epidermal cells. The trichome, which arises from the center of a group of basal cells, is a single thick-walled cell with a neck-like constriction where it passes through the basal cells.

The zone of narrow epidermal cells is limited to those portions of the surface which overlie the vascular bundles; and varies in width depending upon the size of the bundle. The cells are narrow

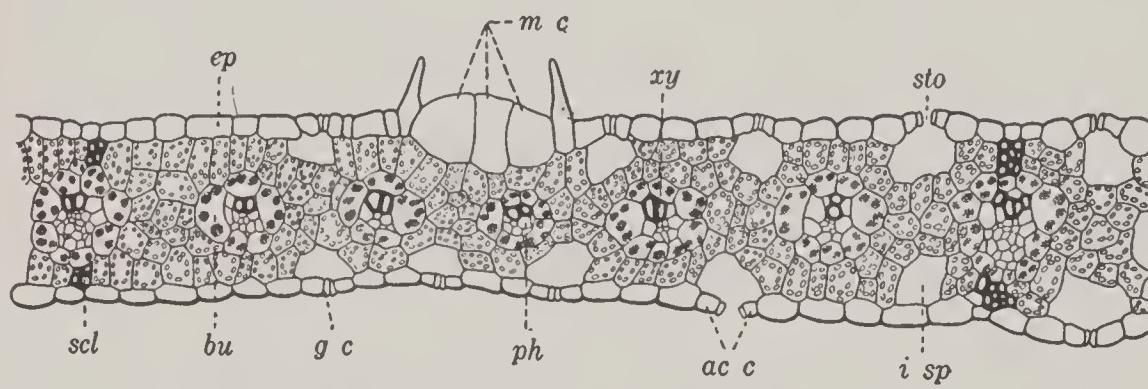


FIG. 52. Transection of a portion of the leaf: *ac c*, accessory cell; *bu*, bundle; *ep*, epidermis; *g c*, guard cell; *i sp*, intercellular space; *m c*, motor cell; *ph*, phloem; *scl*, sclerenchyma; *sto*, stoma; *xy*, xylem. (After Avery.)

with sinuous margins and may lie end to end in a series. Frequently, they are separated from one another by short cells of two kinds — silicified cells and crescent-shaped cells, the latter usually occurring in pairs or in a series of pairs. The silicified cell is two-to four-lobed and may contain crystalline inclusions. The crescent-shaped cells are roughly semilunar, three to five times as wide as long, with walls that are somewhat thinner than those of the adjacent epidermal cells.

The stomatal zone ranges from three to fourteen cells in width and contains epidermal cells with very undulate walls. They may be joined end to end in series; but, more commonly, are separated from one another by two-celled hairs, crescent-shaped cells, silicified cells, horn cells, or the stomatal cells. The two-celled hair is probably a modification of the crescent-shaped cell and is thin-walled with dense cytoplasm. The horn cells are usually confined to the border of the bulliform zone and are fairly thick-walled, frequently being associated with silicified and crescent-shaped

cells. The guard cells of the stomatal apparatus are dumb-bell shaped, and each one is paired with a triangular accessory cell.

Campbell (3) has described the development of the stomata in maize. A vertical wall is formed across the end of an epidermal cell in the stomatal zone, cutting off a daughter cell which is very short. (Fig. 53.) This mother cell lengthens rapidly until it is approximately square in surface outline, and, while it is developing, two small cells at the sides are cut out from laterally adjacent epidermal cells. The accessory cells at first barely keep pace with the growth of the mother cell; but, finally, grow much more

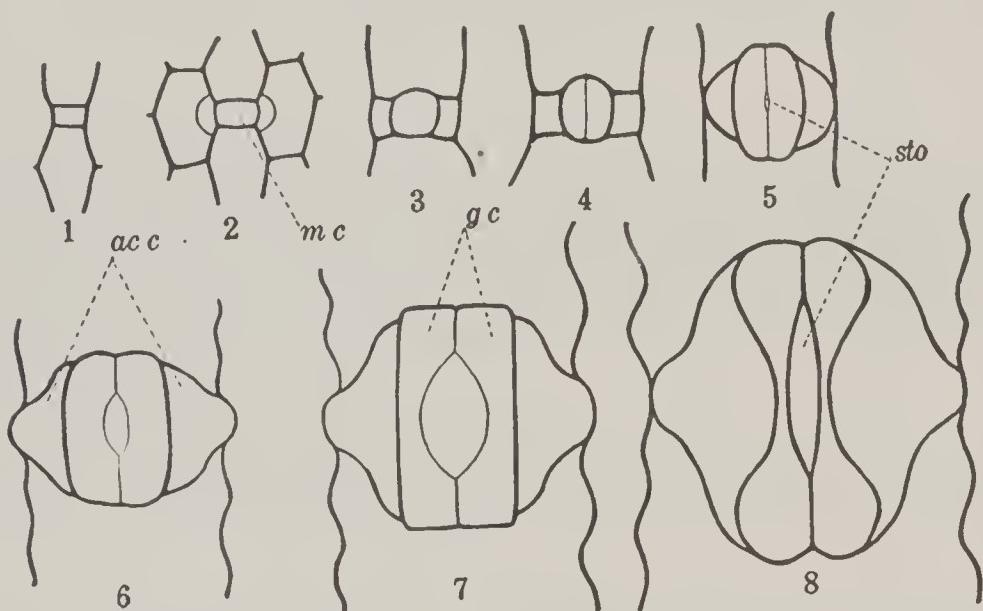


FIG. 53. The development of stoma showing successive stages: *acc c*, accessory cells; *gc*, guard cells; *mc*, mother cell; *sto*, stoma. (After Campbell, *American Naturalist*.)

rapidly and in so doing modify the shape of the guard cells. The mother cell rounds up and divides longitudinally, forming the two guard cells; and, as these lengthen, the accessory cells begin to grow more rapidly and become sub-triangular. The guard cells continue to elongate until they are rectangular and two or three times as long as broad. Meanwhile, the stomatal aperture which is formed schizogenously between the opposing faces of the guard cells elongates, the guard cells attain their final shape, and the accessory cells become larger and more triangular.

THE STAMINATE INFLORESCENCE. — The staminate inflorescence is a broad panicle consisting of a central rachis, which is a continuation of the central axis of the stem, and its lateral branches. (Fig. 54.) The central rachis bears several rows of paired spikelets, while the lateral branches have only two rows of paired spike-

lets. One of the spikelets of each pair is pedicillate, the other sessile. The staminate spikelet may be regarded as the unit of the inflorescence and is normally two-flowered, although one-flowered spikelets have been observed in cases where the second flower is abortive.

At the base of the spikelet are two glumes which subtend and enclose the flowers. Up to the time of anthesis, these are firm



FIG. 54. Staminate inflorescence showing: A, a terminal panicle with its central spike and lateral rachises; B, the paired spikelets; and C, habit of a partially opened spikelet.

and thickly covered with stiff bristle-like hairs with the lower glume overlapping the edges of the upper one. Each flower is subtended by a lemma and a palea, the paleas of the two flowers of the spikelet lying back to back. At the base of each lemma are two lodicules which become very much enlarged at anthesis and hold the glumes open as the filaments elongate. The three stamens are arranged so that two are adjacent to the palea and one is in a dorsal position next to the lemma. The rudimentary carpel is centrally located. The two flowers of the spikelet are identical in structure, but the upper one is the first to mature. Weatherwax (20) has pointed out that the early development of staminate and carpellate

flowers is very similar, "up to the time of differentiation of the primordia of the stamen and pistil." As described by him,

"The spikelet primordium makes its appearance as a rounded protuberance on the rachis. The first differentiation to appear is the formation of the lower glume, and it is soon followed by the upper one. (Fig. 55.) The lemmæ arise almost simultaneously with the appearance of the stamens of the upper flower. From the lower side of the undifferentiated end of the spikelet now appears the primordium of the lower flower and the palea of the upper flower soon follows. The palea of the lower flower appears much later. The older flower *seems* to be terminal and the younger one lateral on the rachilla, but it is probably better to consider both flowers lateral branches of this axis, which terminates between the two paleæ. . . . In the development of the flower from its primordium the stamens are first differentiated; these are followed by the lodicules and the part that is left is the primordium of the pistil. . . . In both flowers of the male spikelet the stamens and lodicules are fully developed but the development of the pistils is soon arrested, and they disorganize."

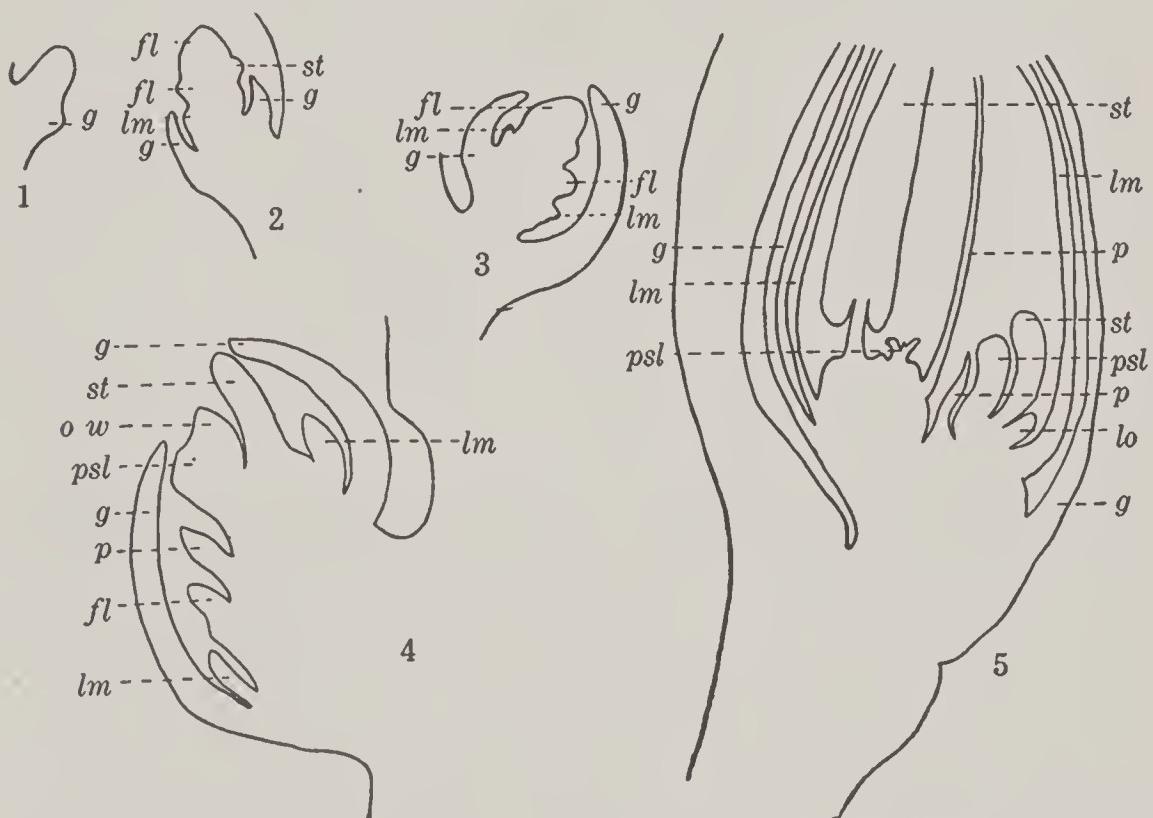


FIG. 55. Diagrams showing details of development of staminate spikelet: *fl*, flower primordium; *g*, glume; *lm*, lemma; *lo*, lodicule; *ow*, ovary wall; *p*, palea; *psl*, pistil; *st*, stamen. (Redrawn after Weatherwax, Bull. Torr. Bot. Club.)

THE CARPELLATE INFLORESCENCE. — The carpellate inflorescence is a thickened spike which ordinarily develops into the ear. Several different views obtain as to the evolutionary development of

this type of inflorescence. One, advanced by Harshberger (8), suggests that the lateral branches or rachids of a primitive inflorescence were united or undiverged to form the ear. On the other hand, Montgomery (11) maintains that only the central spike of the primitive tassel has persisted to form the ear. An alternative theory has been advanced by Collins (5) on the basis of his study of seed hybrids between maize and *Euchlaena*. He suggests that "the shortening and twisting of the axis of a single spike" may be "a possible method of deriving a structure like the maize ear from the inflorescence of *Euchlaena*." In all probability, none of these explanations is complete and a final interpretation must await further studies on the phylogeny of the grasses.

The characteristic two-ranked appearance of the mature grains on the ear is due to the manner in which the spikelets and their flowers develop. This has been fully described by Miller (10) and Weatherwax (19, 20) and the essential details are here summarized. Just back of the meristematic tip of the young axis of the cob, numerous primordia arise on its periphery. Each of these rudimentary primordia, by an equal division, forms a pair of primordial lobes which lie side by side in the same transverse plane; and these in turn develop into the spikelets. The arrangement of the spikelets in transverse pairs is thus the result of the common origin of their primordia from a single rudimentary primordium.

The spikelet is two-flowered, but the lower flower is usually abortive so that a single grain is produced in it. Since the spikelets arise in pairs and a single grain is produced in each one, the grains on the ear have the typical double-rowed arrangement mentioned above. There are some notable exceptions to this arrangement, as in Country Gentleman sweet corn, in which both flowers of the spikelet regularly develop grains. This results in crowding and an irregular arrangement. Other variations include cases in which the grains are paired, connate grains where two kernels are more or less completely united, and anomalous kernels with twin embryos arranged side by side. Stratton (18) studied the development of the double kernel in *Zea Mays* var. *polysperma*. In this case, both flowers of the spikelet are functional and several types of arrangement of the grains occur. In some instances, a pair of separate kernels lie back to back; in others, connate seeds develop with double kernels enclosed in a common pericarp, formed from the coalesced ovaries of the two flowers. Semi-connate types

also occur where the pericarp extends only partially between the kernels.

In the mature carpellate spikelet, like the staminate one, the two flowers are enclosed by a pair of glumes and each flower is subtended by a lemma and palea, these being much shorter than the glumes. The two paleas are back to back and separate the flowers. The sterile (lower) flower has a rudimentary carpel, three rudimentary stamens, and two well-developed lodicules which lie outside of and alternate with the stamens. The fertile (upper) flower has a well-developed carpel, and rudimentary stamens can be distinguished in the early stages of ontogeny. The lodicules of the fertile flower are not easily recognized when the spikelet is mature. The palea and lemma of the lower abortive flower persist and with those of the fertile flower constitute the chaff found at the base of the mature grain.

The sequence of development of the parts of the carpellate spikelet is much like that of the staminate. From the primordium, the lower glume, upper glume, and lemmas of the two flowers are developed in the order named. These are followed closely by the rudiments of the sterile flower and then the rudimentary stamens of the fertile flower appear. The palea of the fertile flower next differentiates and the palea of the sterile flower arises somewhat later.

Following the appearance of the palea and rudimentary stamens of the fertile flower, the carpillary primordium of that flower begins to develop. (Fig. 56.) This arises as a ring from the rounded mass of meristematic tissue which remains after the divergence of the staminal primordia. Growth of this ring is uneven, the side adjacent to the lemma growing rapidly so that it may extend one-third of the way around the young nucellus before the opposite side has begun to develop. The more rapidly growing portion of the ovary wall becomes thicker and more meristematic at its top; and, from this region, the silk or style immediately begins to develop. During the elongation of the style, the ovary wall continues to grow until it completely encloses the ovule except for a small opening at the top of the ovary and adaxial to the style. This opening, which Guignard (7) termed the "stylar canal," later closes as its edges come in contact. These do not unite, however, and the canal can be recognized in the mature ovary.

The silk is solid, somewhat flattened, with two grooves running

longitudinally throughout its length. Two vascular bundles extend from its unequally branched apex through the walls of the ovary to its base, where they are continuous with other bundles supplying the spikelet. These are surrounded by slender sheath cells that are densely cytoplasmic with elongated nuclei. The pollen passes down the silk between these dense cells until it reaches the ovarian cavity. The surface of the silk is hairy; and, throughout most of its length, is receptive to pollen so that the major portion of it may be regarded as a stigma.

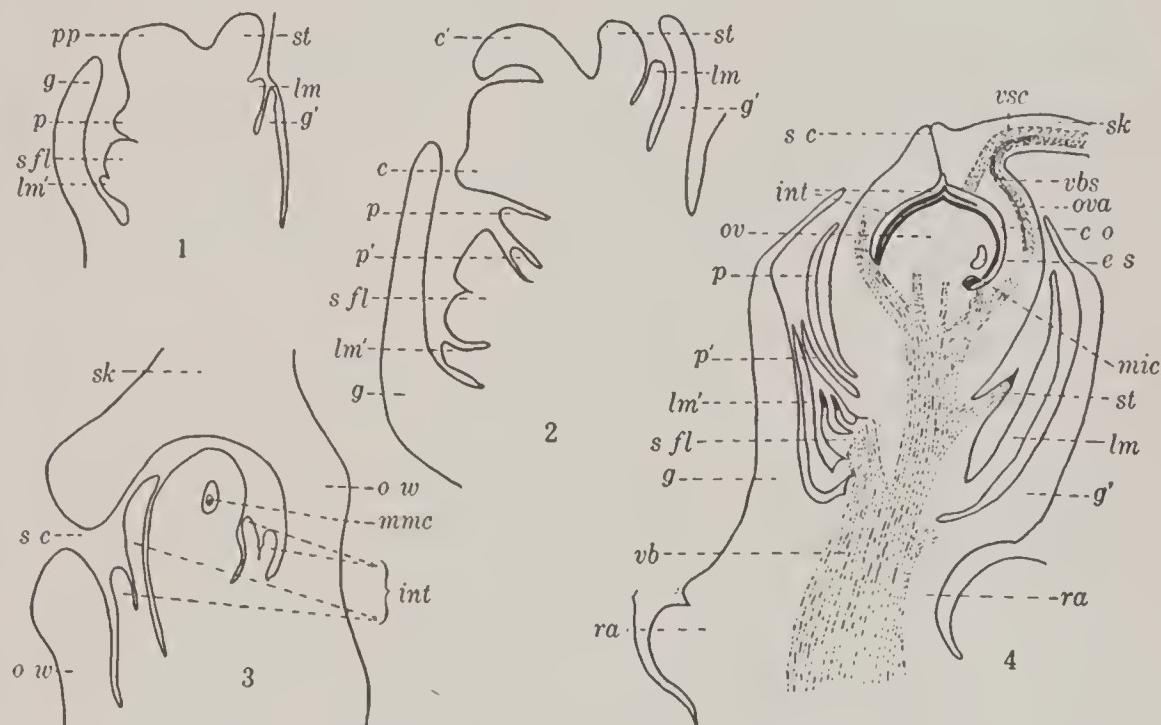


FIG. 56. 1, longisection of young carpellate spikelet; 2, the same, at the time the carpel wall has begun to develop; 3, longisection of the fertile carpel showing nucellus still in erect position; 4, longisection of the carpellate spikelet at the time of pollination: *c* and *c'*, developing ovary walls, *c'* is the portion of the carpel from which the style or silk will develop; *c o*, ovarian cavity; *e s*, embryo sac; *g*, lower glume; *g'*, upper glume; *int*, integuments; *lm*, lemma of fertile flower; *lm'*, lemma of sterile flower; *mic*, micropyle; *mmc*, megaspore mother cell; *ov*, ovule; *ova*, ovary; *o w*, ovary wall; *p*, palea of fertile flower; *'p'*, palea of sterile flower; *pp*, primordium of carpel; *ra*, rachilla; *s c*, stilar canal; *s fl*, sterile flower; *sk*, silk or style; *st*, rudimentary stamen; *vb*, vascular bundle; *vbs*, one of the vascular bundles of the silk; *vsc*, sheath cells of the silk. (Diagram 4 reduced to approximately one-sixth the size of diagrams 1-3. Redrawn after Miller, *Jour. Agr. Res.*)

DEVELOPMENT OF THE OVULE. — Although the older interpretation that the pistil consists of a single carpel is accepted by some morphologists, the more generally held view is that it is tri-carpellate. Randolph (15) has summarized this concept in describing the formation of the ovary and the development of the ovule. The ovary consists of three undiverged carpels, and a single ovule arises near the base of the ovary on the side adjacent to the rachilla.

The midribs of the bundles of the lateral carpels extend into the silk, their marginal bundles supplying the ovule. The third carpel, which is regarded as rudimentary, has a vestigial median bundle that is sometimes present at the base of the ovary opposite the point of divergence of the ovule. The nucellus arises in an erect position; and, shortly before the megasporangium mother cell is differentiated, there is an acceleration of cell division and growth on the side of the nucellus adjacent to the palea. As a result of this differential growth, the ovule finally becomes semianatropous or approximately campylotropous. There is no well-defined funiculus at the broad base of the ovule, and the two integuments which are initiated at this point are free from each other. The inner integument completely surrounds the nucellus except at the micropyle; but the outer one extends only partially around it, forming a wedge-shaped angle where it projects into the funnel-like depression of the stylar canal. (Fig. 56-4.)

THE MEGAGAMETOPHYTE. — Megasporogenesis occurs at about the time that the ovule begins to curve. The megasporangium mother cell is then differentiated and subsequently four megasporangia are produced, the innermost one being functional. When the megagametophyte reaches the eight-nucleate stage, two polar nuclei move to the center of the embryo sac; but they do not completely fuse prior to fertilization. The three antipodal nuclei begin to divide at once, and the number increases until as many as 24 to 36 cells are formed which may be binucleate. Meanwhile, the synergids become elongated or lunar-shaped with very dense contents. In most instances, they do not remain intact after the time for fertilization has arrived and usually disintegrate prior to that event. The megagamete increases in size until its width is approximately half that of the embryo sac.

THE MICROGAMETOPHYTE AND POLLINATION. — The development of the stamens is like that of other grasses; and, following reduction division, the pollen matures to form grains that are almost spherical, with a minutely roughened exine and a prominent germ pore. A thickened ring of the intine surrounds the pore and closes it with a plate of tissue that resembles the rest of the wall in structure. The pollen grain, now a microgametophyte, has dense protoplasm and contains a vegetative and a generative nucleus. Before shedding, the latter divides to form two long, slender microgametes that are crescent-shaped and pointed at the ends.

The fine, light pollen is well adapted to wind pollination. Gravity may play some part in the process, but it is unlikely that many insects act as pollinating agents. A few hours after the pollen grain lodges on the hairs of the silk, the pollen tube pushes through the germ pore and gains access to the sheath cells adjacent to the vascular bundles of the silk. Practically all functional pollen tubes develop from pollen grains that are lodged on the multicellular hairs of the silk, although occasionally penetration may be other than through a hair. Growth of the pollen tube in the silk is very rapid and it may reach the embryo sac within twenty-four hours after pollination. Upon the entrance of the pollen into the embryo sac, fertilization is effected. This is double in character, one microgamete uniting with the megagamete to form the zygote, and the other with the polar nuclei to form the primary endosperm nucleus. The latter undergoes division directly after fusion; and, as a result of several free nuclear divisions, there are usually four to eight endosperm nuclei formed before the division of the zygote takes place.

EMBRYOGENY. — The zygote divides into two unequal cells about 28 to 34 hours after pollination; and further divisions of the smaller apical cell form the embryo, while the basal cell divides to form a massive suspensor. The subsequent development has been described in detail by Randolph (15). He observed three- or four-celled embryos 36 hours after pollination; and at the end of four days, they usually were comprised of from 10 to 24 cells. Unlike the ontogeny of many grass embryos, there is little regularity in the sequence of cell divisions or arrangement of the cells in tiers, so that the proembryo cannot be described as conforming to a regular pattern.

From the fourth to eighth days, growth is restricted chiefly to the apical region, there being few divisions of the suspensor; and, as a result of this differential growth, the embryo becomes club-shaped. About eight days after pollination, the epidermis is differentiated in the apical portion of the embryo and extends toward the suspensor.

The axis of the more mature embryo can be determined in about ten days, when a slight protuberance is formed on the anterior surface of the proembryo. This represents the apex of the stem axis of the embryo and is oriented at an oblique angle to the proembryo. During the period from ten to fourteen days after pollina-

tion, the meristems of the primary root and epicotyl are differentiated, the scutellum enlarges, and there is also considerable growth of the suspensor. In the ensuing week, the primordia of the coleoptile and first foliage leaves arise, which usually number five by the time the embryo is mature. The suspensor ceases to enlarge after about twenty days. (Fig. 57.)

The growth of the embryo is rapid during the next three weeks; and, at the end of about forty-five days, it is morphologically mature. The coleoptile is differentiated as a closed sheath about

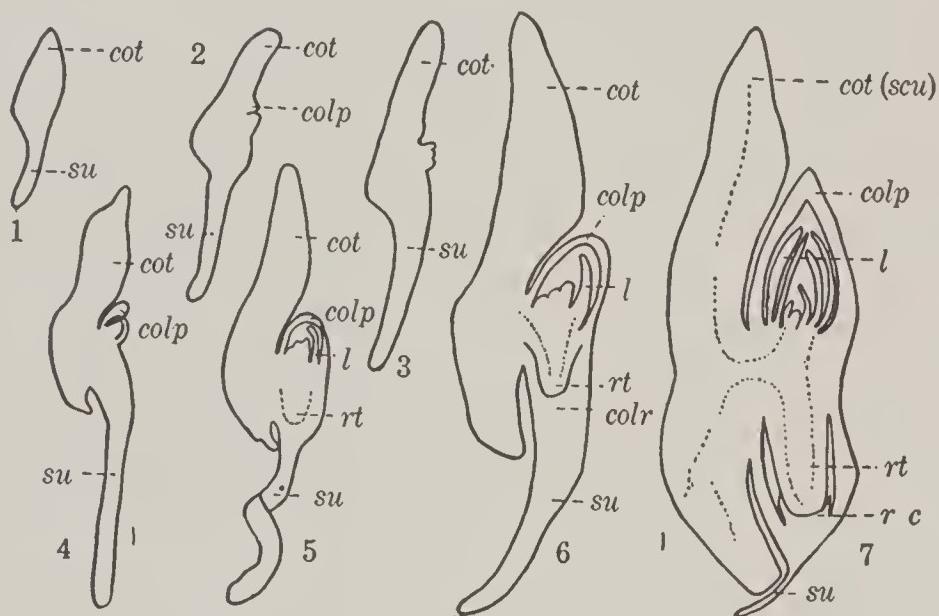


FIG. 57. Diagrams 1-6, steps in the development of the embryo; 7, longisection of nearly mature embryo, reduced one-half: *colp*, coleoptile; *colr*, coleorhiza; *cot*, cotyledon or scutellum; *l*, leaf; *rc*, root cap; *rt*, root; *su*, suspensor. (Redrawn after Weatherwax, *The Story of Maize*, Univ. of Chicago Press.)

the young foliage leaves; and the portion of the axis between the suspensor and the cotyledonary node forms the primary root within the surrounding tissue of the coleorhiza. The differentiation of two or more seminal roots just above the cotyledonary node completes the ontogeny of the embryo.

THE ENDOSPERM. — According to Randolph, the primary endosperm nucleus undergoes division prior to that of the zygote, and free nuclear divisions occur so that three days after pollination approximately 128 free nuclei may be present. Shortly after this time, wall formation is initiated in the endosperm adjacent to the embryo and it becomes almost completely cellular by the end of four days, except in the antipodal region. The size and shape of the endosperm changes rapidly thereafter, and the dimensions of the

mature endosperm are approximately fifty times that of its initial stage. This growth is accomplished by a general cell division of the parenchymatous cells; but, later, there is a localization of this activity to the peripheral region of the endosperm. The outermost layer of the endosperm, which forms the aleurone zone, exhibits certain epidermal characteristics; and, after about three weeks, divides only anticlinally. The subepidermal cells may continue to divide until the embryo is mature and are consequently smaller than the aleurone cells.

THE ANTIPODAL TISSUE. — The persistence of antipodal tissue has been noted by Weatherwax (23) and Randolph (15). In many grasses, the antipodals are reported as disintegrating during the formation of the endosperm; but in corn, this haploid tissue (10 chromosomes) persists until the caryopsis is mature. It occupies a position near the micropyle during the early ontogeny; but as the endosperm enlarges is displaced and comes to occupy a region in the crown of the kernel. At maturity, the antipodal tissue consists of hundreds of cells, which are packed with starch, surrounded by an epidermis that is starch-free.

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CHAPTER VI

GRAMINEAE — *Continued*

TRITICUM spp.

WHEAT is grown in the temperate regions of every continent, within the Arctic Circle, and in the highlands of Ecuador and Colombia at the Equator. In the United States, it is a winter or summer annual, being harvested in the southern states in June and in the northern wheat areas in July and August.

There has been much discussion as to the origin of wheat; and, although some botanists maintain that all cultivated forms are derived from a single wild ancestor, the majority, according to Percival (10), "agree that the wheats are polyphyletic, and that at least two species are concerned in their origin." Several systems of classification have been proposed for the numerous species, races, and varieties which are recognized at the present time. Hackel (6) has divided the genus into two sections, *Aegilops* and *Sitopyros*; and the latter, which includes the cultivated wheats, into three main species. The first of these is *T. monococcum* L., commonly known as Einkorn or one-kerneled wheat, which is cultivated in Spain and probably grows wild in Greece and Mesopotamia. The second, *T. sativum* Lam., is the commonly cultivated wheat, which he further subdivides into three principal races: *T. spelta* L., which includes the ordinary spelt wheats; *T. dicoccum* Schr., emmer wheat; and *T. tenax*. The last named has four subraces: *T. vulgare* Vill., common wheat; *T. compactum* Host., club wheat; *T. turgidum* L., poulard wheat; and *T. durum* Desf., durum wheat. The third main species is *T. polonicum* L., Polish wheat, which is not a native of Poland, but occurs in Italy and Abyssinia and is cultivated to some extent in North America.

Percival recognizes two wild species, and classifies the cultivated wheats in eleven natural groups or races of major rank. Of these, the common bread wheat, *Triticum vulgare*, is the best known and most generally used. This may be attributed to its physical

qualities, which are suited to bread-making, and to its adaptability to a variety of climatic conditions, which has resulted in its being the most widespread of all cultivated forms. For this reason, the following account is based upon *T. vulgare* unless otherwise stated.

GENERAL MORPHOLOGY

THE ROOT SYSTEM. — The root system is dual, consisting of a primary seminal system and a permanent adventitious one which

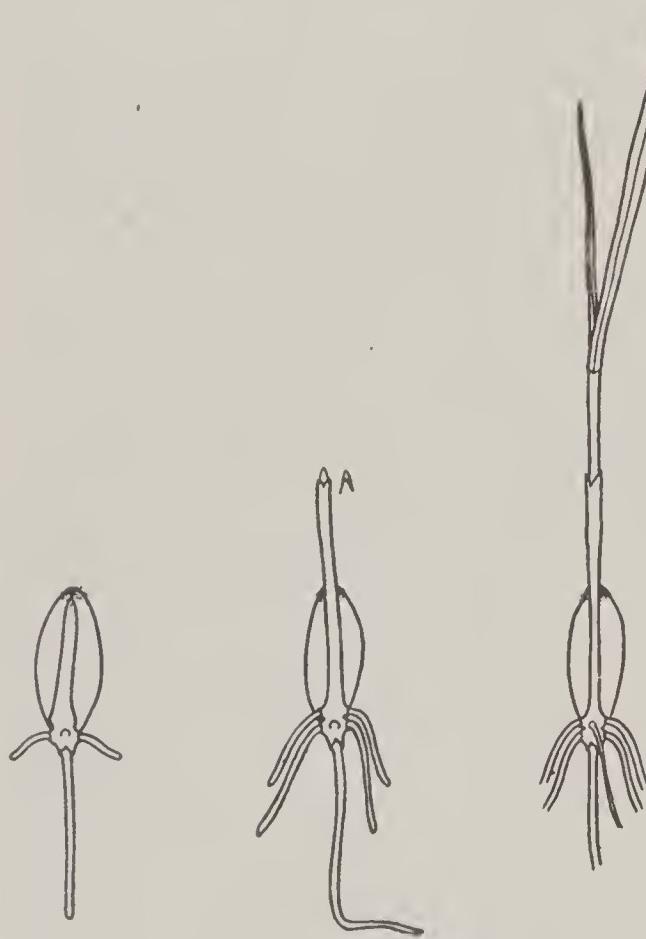


FIG. 58. Stages in the development of the seedling.
(After Avery.)

forms a deeply penetrating, widely spread, and profusely branched system of fibrous roots. The primary system typically consists of five roots, the tap root and two pairs of laterals which arise in the region of the vascular plate of the scutellar node. (Fig. 58.) When a sixth root arises, it occurs at a point near the base of the coleoptile adjacent to the epiblast; and a third pair of rootlets sometimes develops at the first internode above the second pair and in the same plane with them. All the seminal roots are slender, of uniform diameter, and produce fine lateral branches.

The primary roots do not form a large proportion of the total root system; but, under favorable conditions, they penetrate the soil to a depth of 8 to 12 inches or more; and may persist throughout the entire life of the plant. In fact, McCall (9) has pointed out that the subcrown root system is capable of carrying the plant to complete maturity, and Locke and Clark (8) have reported instances under certain arid conditions where the root system consisted entirely of seminal roots. In such cases, the plant does not tiller to any extent; and only the main culm develops, which,

though reduced in size, is normal but tends to lodge, owing to the absence of the support usually afforded by crown roots.

The permanent root system is comprised of whorls of adventitious roots which arise from the lower nodal regions of the main stem and its branches near the soil level. The first adventitious roots appear at the tillering node about an inch below the soil level, and consist of a pair of roots arising at right angles to the plane of phyllotaxy and parallel to the plane of the three pairs of seminal roots. Another pair is formed at the second node in similar manner; but, near the ground level, where the internodes are longer, the whorls may consist of four to six roots arranged in pairs. Each secondary axis produces its adventitious system in a manner similar to that of the main culm, except that a single root instead of a pair is usually produced at the base of each secondary or subsequent lateral axis.

The rapidity and extent of development of the adventitious roots vary with cultural conditions and practice. Weaver (15) has investigated this point; and finds that, under favorable conditions, root elongation is very rapid, being maintained in some cases at the rate of half an inch a day for 60 or 70 days in winter wheat. In describing the root system of spring wheat, he states,

"The roots of the secondary system ramify the soil near the surface 6 to 9 inches on all sides, and likewise fill the 2 to 3 feet below this area with a network of well-branched roots. Winter varieties are similar in general habit but more deeply rooted. Crops planted early during seasons favorable for growth form a secondary root system which rather thoroughly fills the surface 12 to 20 inches of soil, while the primary roots extend well into the third and fourth foot. The mature root system has a working level of 3.5 to 4 feet and a maximum depth of 5 to 7 feet."

The degree of branching and depth of penetration are subject to great modification, depending upon the type of the subsoil, the amount of moisture and aeration, and the character of the fertilizer applied to the soil. (Fig. 59.)

THE STEM. — The jointed, cylindrical stems or culms are smooth or scabrous, and contracted at the nodes, which are solid. The internodal portions are hollow at maturity, except in some varieties of macaroni and poulard wheats in which there is a persistent pith. The total height may vary from 2 to 5 feet, being even shorter in some of the dry land areas; and there are usually about six inter-

nodes, although five or seven are not uncommon. The basal internode remains short, while the second one elongates so that

the first adventitious roots of the secondary root system are about an inch below the surface of the soil. The internodes above the second are successively longer, the uppermost one which bears the terminal spike being the longest. The diameter of the stem is influenced by various factors; but it increases up to the fifth internode, while the sixth is more slender than the rest.

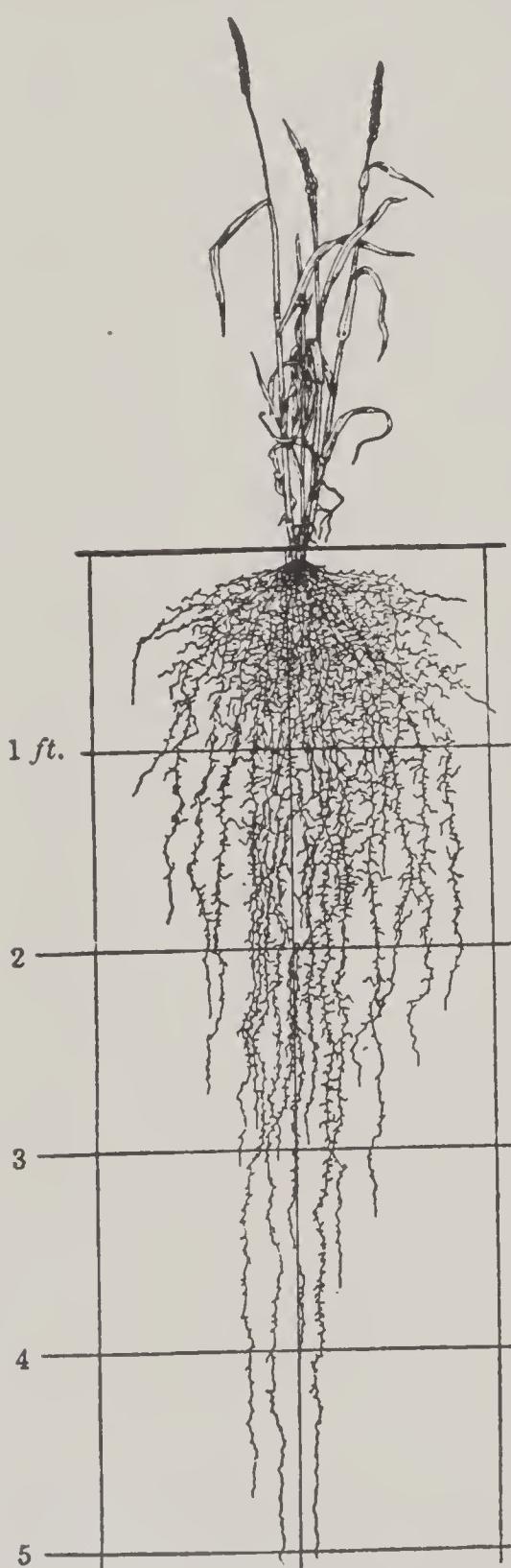


FIG. 59. The root system at the time of blossoming. (From Weaver, *Root Development of Field Crops*. McGraw-Hill Book Co.)

Secondary shoots or tillers arise from axillary buds at the basal nodes of the main axis; and from these lateral culms, still others may develop. In this manner, the process of tillering results in the formation of several axes of the second and third order until many branches have been produced. The behavior of the axillary buds in forming tillers depends in part on the depth of planting of the grain. When the depth is less than 2 inches, the bud in the axil of the first foliage leaf develops immediately; at about 2 inches, the third axillary bud is usually the first to grow vigorously; and where planting is 3 or more inches deep, the first three buds of the main axis remain dormant or grow weakly, while the fourth lateral bud produces a strong stem.

THE LEAVES. — The alternate, two-ranked leaves are of several kinds: (1) the seedling leaves (scutellum and coleoptile); (2) the

prophylls of the lateral branches; (3) the foliage leaves; and (4) the glumes of the inflorescence. The seedling leaves are described in connection with the structure of the embryo and the germination of the seedling.

The first leaf or prophyll of a lateral shoot is binerved, resembling the coleoptile in its conical form and in the apical opening through which the succeeding foliage leaves emerge. It attains a length of an inch or more, and its upper portion is green with deflexed hairs along the two veins. The prophyll is oriented so that its concave or flattened surface opposes the axis from which the shoot enclosed by it arises; but the next leaf is diverged at a 90° angle from the prophyll, and each succeeding one has a divergence of 180° , so that the plane of phyllotaxy is at right angles to that of the axis from which the shoot is diverged.

The foliage leaf consists of the sheath, blade, and ligule. The sheath encloses the culm, being entire near its base; but its upper part is open on the side distal to the blade, and the outer of the two overlapping edges is slightly raised. The lamina is variable in shape, being narrowly linear to linear-lanceolate, and frequently twisted, the torsion being to the right. The venation is parallel, and the bundles are reinforced by mechanical tissue which gives support to the blade, while further stiffening may result from the presence of silica in the epidermis. The curling or expanding of the blade along its longitudinal axis is controlled by the presence of bulliform or motor cells on the adaxial surface. Stomata occur on both surfaces, but with greater frequency on the adaxial one in a ratio of approximately 10 to 7. The claw-like auricles which develop at the base of the blade, where they loosely clasp the sheath and the stem, are somewhat larger than those of rye and not as prominent as those of barley. In young wheat plants, they are frequently somewhat pubescent; and at maturity the tips and margins may have a few unicellular hairs. The ligule, which arises at the junction of the blade and the sheath and surrounds the stem, is a thin, colorless, membranous structure with an irregular edge that is fringed with small hairs.

THE INFLORESCENCE. — The inflorescence is a compound spike which is usually 3 to 4 inches in length, but may vary from 2 to 5 inches. (Fig. 60.) It may differ greatly in its shape and degree of compactness, the density of the spike being determined in part by the length of the internodes and the distribution of the spikelets.



FIG. 60. Habit of the mature spike of *Triticum vulgare*, Vill., Portage variety. (Photograph by J. Horace McFarland Co.)

In most cases, this is uniform, but where the spikelets are crowded at the tip, the spike becomes clubbed. It consists of a zigzag central axis or rachis, and lateral spikelets which arise in two rows from each notch or node of the central stalk. (Fig. 61, A, B.) There is a fertile terminal spikelet which is placed at right angles to the others. Each joint of the rachis is flattened on one side, somewhat concave on the other, and broader at the apex than at its base. The sessile spikelets lie against the concave surface of each joint of the rachis in an alternate arrangement.

Grantham and Frazier (5) report that

"the average spike of wheat (*Triticum spp.*) contains from fifteen to twenty spikelets each of which under favorable conditions is capable of producing two or more kernels. Ordinarily, however, the lower two or three spikelets on the spike do not develop."

In the bearded varieties the percentage of sterile spikelets is higher than in the beardless ones.

Percival (10) has described the structure of the rachis, which resembles that of the internodes of the culm. Its upper internodes are flattened and spindle-shaped in transection, while the lower ones are somewhat semicircular. The epidermal cells are oblong with sinuous, thickened walls which alternate with oval or kidney-shaped "dwarf" cells; and at the edges of the rachis are unicellular epidermal hairs. Stomata occur in rows and overlie longitudinal zones of chlorenchyma which are found only on the convex surface of the rachis; while, on the flattened surface, there is a band of subepidermal mechanical tissue. The center of the rachis is parenchymatous and the large vascular bundles are arranged in a circle with the smaller ones disposed on the inner face of the chlorenchyma. The rachilla is similar in structure to the rachis but much more slender and usually contains three vascular bundles.

THE SPIKELET. — The spikelet is the unit of the inflorescence, and consists of from two to nine flowers which arise from an unelongated axis or rachilla in a distichous arrangement corresponding to the phyllotaxy of the vegetative axis. (Fig. 61, A, B.) They are subtended by overlapping bracts or glumes which resemble the sheath of the foliage leaf in general structure, and the two lowermost ones do not have flowers in their axils. The slightly crowded flowers of each spikelet are completely enclosed by the glumes until anthesis. One or more of the upper flowers are

usually sterile and imperfect, so that only two or three kernels are matured except in some of the club wheats, in which the spikelet may contain five or more. On the average, each spikelet has four flowers and produces two mature grains.

Each bract, aside from the two sterile basal glumes, is known as a lemma and bears a flower in its axis. The lemma may be beardless,

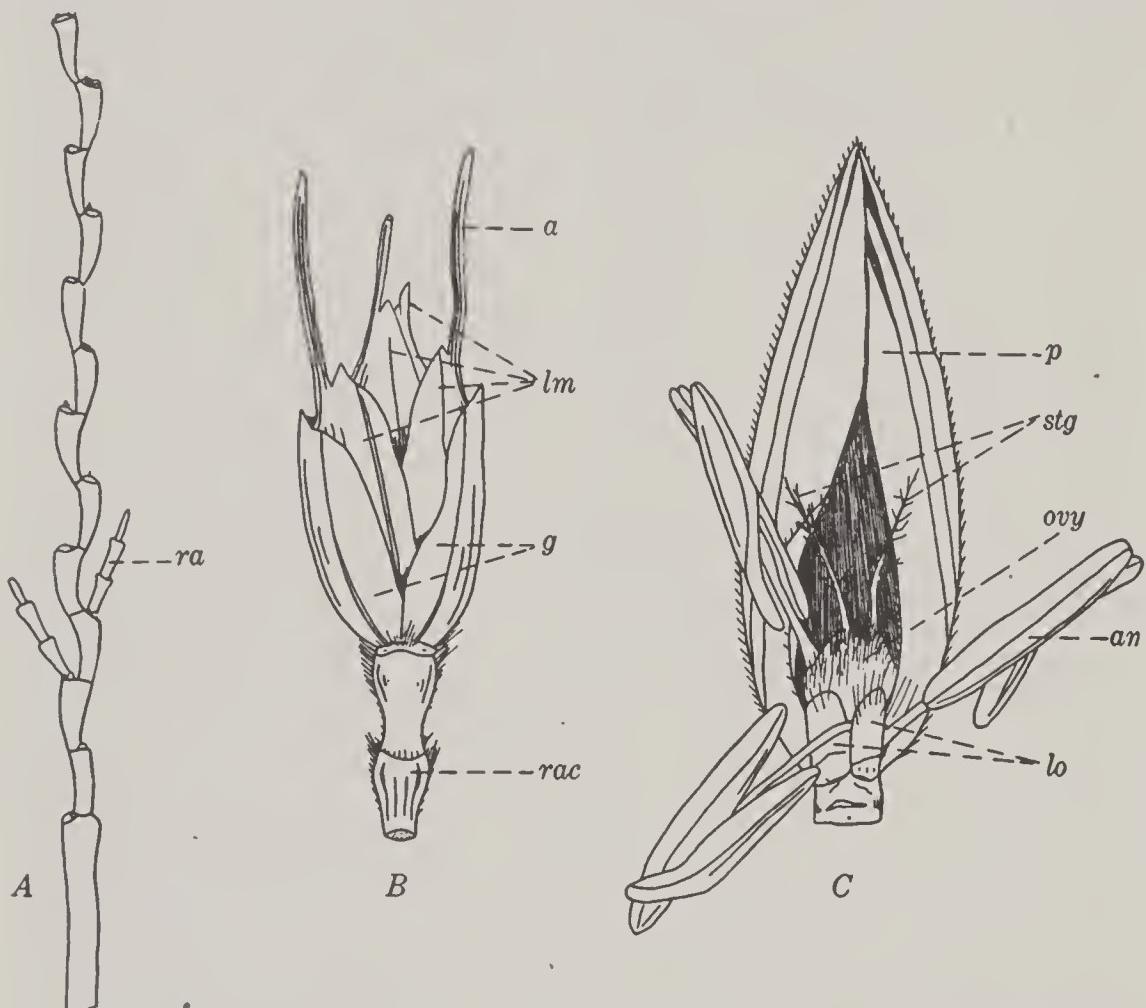


FIG. 61. *A*, the rachis of the inflorescence showing the rachilla, *ra*; *B*, a single spikelet; *C*, a flower with the lemma removed and the palea drawn back to expose the enclosed floral parts: *a*, awn; *an*, anther; *g*, glumes; *lm*, lemmas; *lo*, lodicules; *ovy*, ovary; *p*, palea; *rac*, rachis; *stg*, stigmas. (*A*, redrawn from Percival, *The Wheat Plant*, Duckworth and Co.; *B* and *C*, redrawn from Robbins, *Botany of Crop Plants*, P. Blakiston's Son and Co.)

although few wheats are strictly so; or bearded with a terminal awn that tapers from base to tip and is sub-triangular in transection. Its epidermis like that of the glume is comprised of elongated cells with sinuous walls, and oval ones that are often papillate. The fine pointed, thick-walled hairs are directed toward the apex of the awn and give it a scabrous character. Stomata occur in rows on the outer face of the awn; and underlying them are zones of chlorenchyma, while the angles are reinforced by bands of mechanical

tissue. One large and two smaller vascular bundles are present, the former being continuous with the midrib of the glume.

Opposite to and enclosed by the lemma, with its abaxial surface toward the rachilla, is the palea, which is diverged from a very short pedicel or flower stalk. (Fig. 61, C.) This is an awnless, two-keeled bract of thinner texture than the lemma, having transparent, infolded margins. Enclosed by it are the three stamens and single pistil, as well as two small, ovate, membranous scales, called the lodicules, which lie on the opposite side of the pedicel from the palea and near the base of the ovary. The large anthers are sagittate, and the cylindrical filaments have a single vascular strand. The ovary is one-celled, covered with down at its apex, and surmounted by two short styles which terminate in feathery, brush-like, stigmatic branches.

At anthesis, the swelling of the lodicules results in the pushing apart of the lemma and palea; and the filaments elongate rapidly, carrying the anthers up and outside of the glume. Dehiscence begins before the flowers are fully open, continuing until they again close; and, in most wheats, close pollination occurs although there may be a small percentage of natural crossing. The latter is commonly the case in durum wheat.

ANATOMY

THE MATURE GRAIN. — The mature grain or fruit is a caryopsis. The pericarp and the remains of the integuments of the single seed are so closely adherent that they cannot be readily separated from each other at maturity. The grain is ovate with a furrow or crease on the surface facing the palea which is caused by an infolding of the lateral portions as maturation and desiccation proceed. The surface of the grain is smooth except at the stigmatic end, where there is a brush or tuft of persistent hairs. These become thick-walled and rigid surrounding the styles which may sometimes persist. (Fig. 62.) The embryo develops at the base of the fruit on the side away from the groove, and may be located externally by the wrinkled surface of that portion of the pericarp which overlies it.

The histology of the grain has been investigated by Bessey (2), Percival (10), Tschirch and Oesterle (14), Winton (16), and others. It may be divided into three main regions: (1) the bran layer including the pericarp, remains of the seed coat and nucellus;

(2) the endosperm; (3) the embryo. There are usually five layers or zones of cells in the pericarp. These in order from the outer surface are: (1) the epicarp or outer epidermis; (2) the hypodermal parenchyma; (3) the cross cells; (4) the intermediate cells; and (5) the tube cells.

The cells of the epicarp are elongated parallel to the long axis of the grain, and have pitted walls that are much thickened and cutinized, appearing beaded in surface view. At the apex, the cells are more polygonal; and some of them develop as epidermal hairs which are thick-walled, pointed, and broad or bulbous at



FIG. 62. The grain of wheat and early stages in germination.

the base. Beneath the epicarp are one or two layers of elongated hypodermal cells which resemble those of the former. The cells of both epicarp and hypodermis become much compressed, and their walls are so heavily thickened at maturity that the cell cavities are not easily distinguishable. Underlying this layer, there may be some thin-walled intermediate cells associated with cross cells, the latter being so named because they are oriented with their long axes at right angles to the outer layers of the pericarp. The cross cells have characteristic transverse pits and contain chlorophyll when the grain is young. The tube cells make up the inner epidermis of the pericarp, and underlie the cross cells, forming a spongy parenchyma in which there are numerous intercellular

spaces. Their long axes are parallel to those of the cells of the epicarp; and, because of their loose arrangement, they appear as rings in transection. (Fig. 63.)

The seed coat is much crushed at maturity, and appears as a zone of cells in which the walls can scarcely be distinguished. Its ontogeny is described in connection with the development of the ovule and embryogeny. The nucellar tissue or perisperm is, for the most part, resorbed in the development of the grain, and may be completely absent at maturity. When present, it consists of one

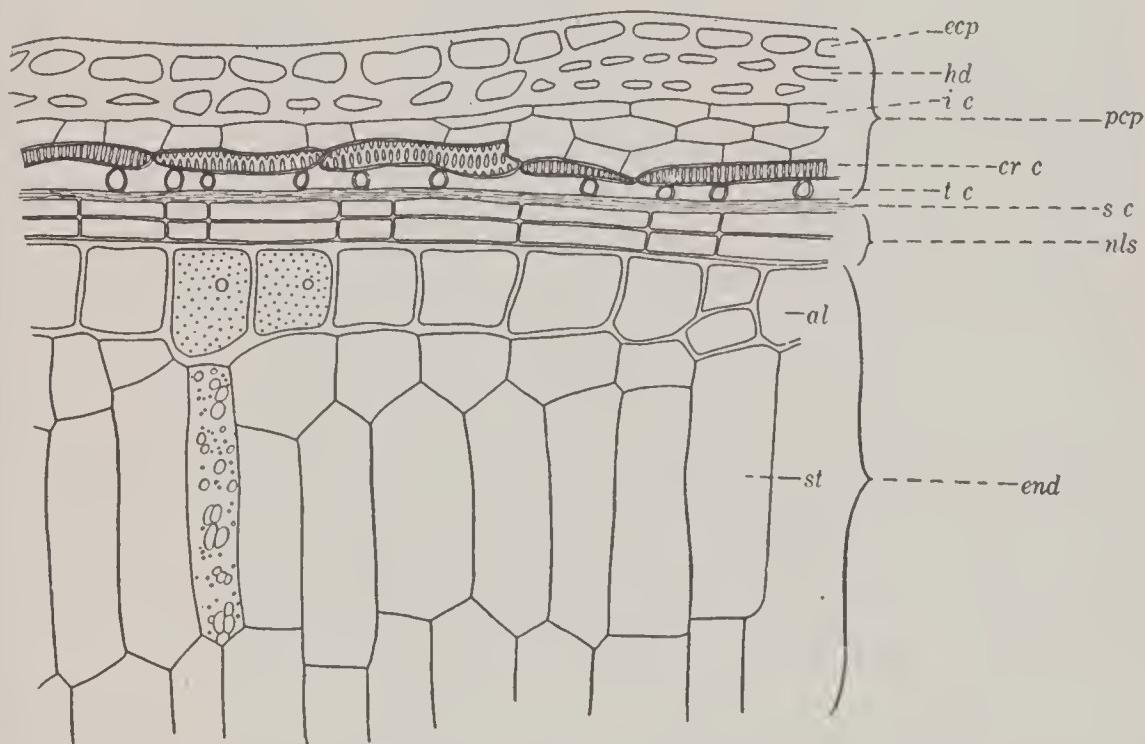


FIG. 63. Transection of a portion of a mature grain showing detail of pericarp, integuments, nucellus and endosperm: *al*, aleurone layer; *cr c*, cross cells; *ep*, epicarp; *end*, endosperm; *hd*, hypodermis; *ic*, intermediate cells; *nls*, nucellus; *pcp*, pericarp; *sc*, seed coat; *st*, starchy endosperm; *tc*, tube cells. (Redrawn from Tschirch and Oesterle, *Anatomischer Atlas der Pharmakognosie und Nah rungsmittelkunde*, Herm. Tauchnitz.)

or two layers of cells with thickened walls which overlie the aleurone cells; and, in the mature grain, they are commonly crushed so as to form a bright colorless line, the hyaline layer. The aleurone cells constitute the outer zone of the endosperm, which is usually a single layer except in the region of the furrow; and the thick-walled cells appear square or rectangular in a transection of the grain, being more or less rounded to polygonal in surface view. They contain an abundance of protein granules and some fat. The protein appears to be formed by condensation processes during the desiccation of the wheat kernel.

The starchy endosperm constitutes the main bulk of the grain, and its cells are thin-walled, with their long axes at right angles to the surface of the grain. They are filled with starch and contain all of the gluten found in the endosperm. The lenticular starch grains are intermediate in size between the larger ones found in rye and the smaller ones which occur in barley. The endosperm, including the aleurone layer, constitutes approximately 85 to 90 per cent of the entire bulk of the mature grain, the embryo about 6 per cent, and the bran layer the remainder.

THE EMBRYO. — The mature embryo lies embedded in the endosperm slightly to one side and at the base of the grain opposite the groove. The embryonic axis consists of the primary root, enclosed by the root sheath or coleorhiza; the epicotyledonary portion of the axis, enclosed by the coleoptile; and two lateral divergences, the scutellum and the epiblast. (Fig. 64.) The scutellum is the large, lateral, shield-shaped cotyledon which slightly exceeds the embryonic axis in length. Its convex, abaxial surface lies in close contact with the starchy cells of the endosperm; and the epidermal cells are elongated at right angles to the surface of the scutellum, constituting an epithelial layer which is secretory in function. In some varieties, invaginations occur in the surface, but this is not as common as in corn. The scutellum partially surrounds the coleoptile and extends slightly beyond it so that a projection is formed, known as the ventral scale, which overhangs the coleoptile. The epiblast is a small non-vascular outgrowth which arises in the region of the cotyledonary node on the side of the axis distal to the scutellum.

The conical coleoptile is entirely closed except just below the tip, where there is a slit-like pore away from the scutellum; and enclosed by it are the primordia of two or three foliage leaves. The first foliage leaf is diverged from the axis on the side opposite the scutellum, and succeeding leaves have a similar angular divergence of 180° . A lateral bud is developed in the axil of the coleoptile on the side adjacent to the scutellum.

THE VASCULAR SYSTEM OF THE EMBRYO. — The vascular strands of the embryo consist of elongated thin-walled conducting elements, and the scutellum is supplied with a broad strand which is directed towards its tip, branching frequently at its upper limits so that a fan-like system is formed. The small branches curve to

the right and left, extending downward almost to the base of the scutellum. The scutellar bundle enters the axis at the cotyledonary

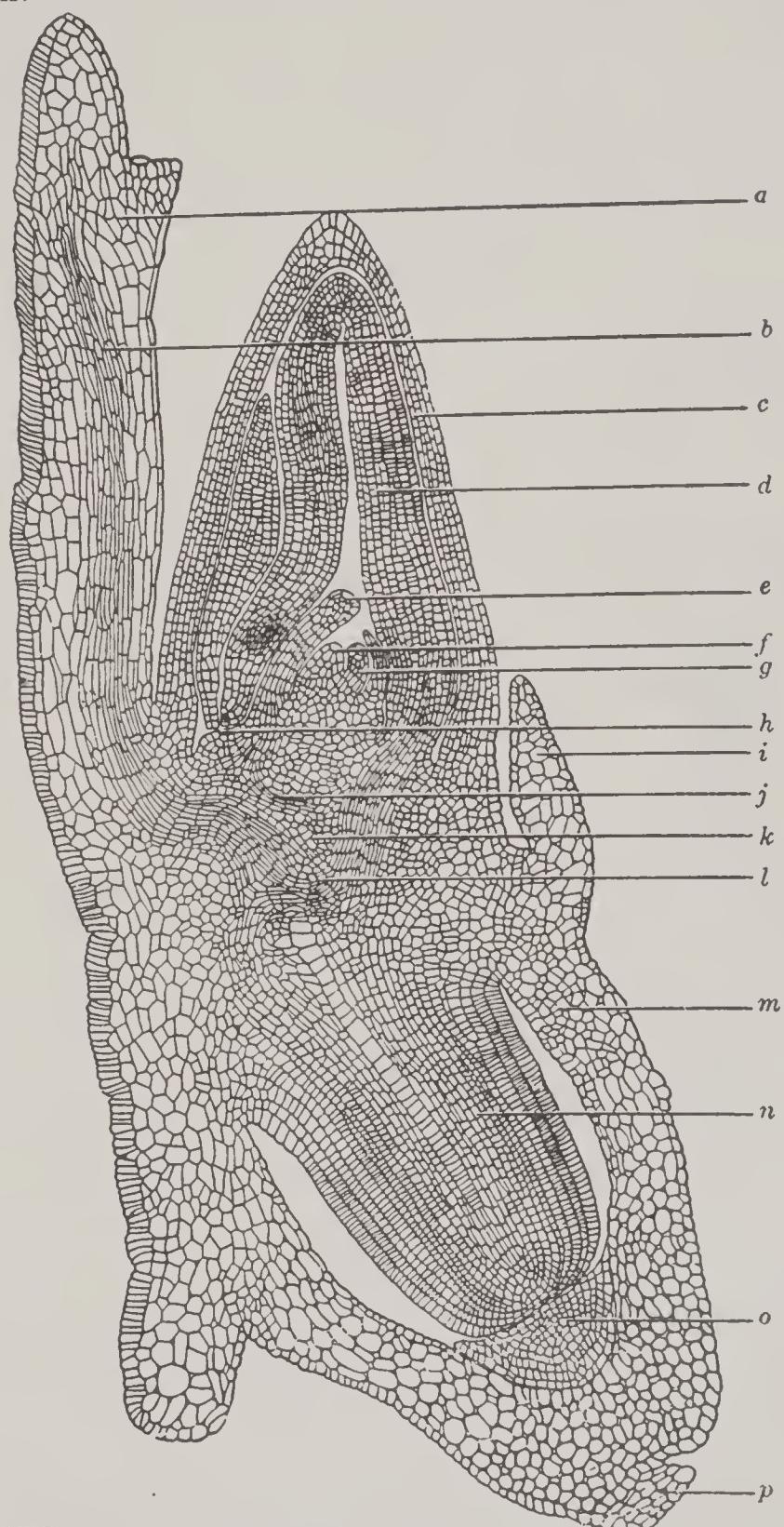


FIG. 64. Median longisection of a wheat embryo (Turkey variety): *a*, ventral scale of scutellum; *b*, scutellar trace; *c*, coleoptile; *d*, first foliage leaf; *e*, second foliage leaf; *f*, growing point; *g*, third foliage leaf; *h*, bud in axil of coleoptile; *i*, epiblast; *j*, procambial strand; *k*, first internode; *l*, cotyledonary node; *m*, coleorhiza; *n*, primary root; *o*, root cap; *p*, remains of suspensor. (After McCall, *Jour. Agr. Res.*)

node and may extend up the first internode a short distance before becoming a part of the stele. (Fig. 65.)

According to Avery (1), the median third of the scutellar bundle becomes a part of the stele directly; and extends downward as a part of it to the scutellar node, where it turns upward. At the point of upward curvature, vascular strands from the root anastomose with it, and the combined strand becomes the midrib of the foliage leaf above the coleoptile. (Fig. 66.) Each of the outer branches proceeds laterally upward and again forks to form two bundles, the outer one of each pair being a coleoptilar trace. In *T. vulgare*, two unbranched bundles pass from the base to the apex of the coleoptile; but in some species of *Triticum*, as many as six have been reported by Percival (11).

The inner bundle of each pair, after passing upward in the axis, branches and gives rise to one or more bundles which constitute the trace of the first foliage leaf above the coleoptile.

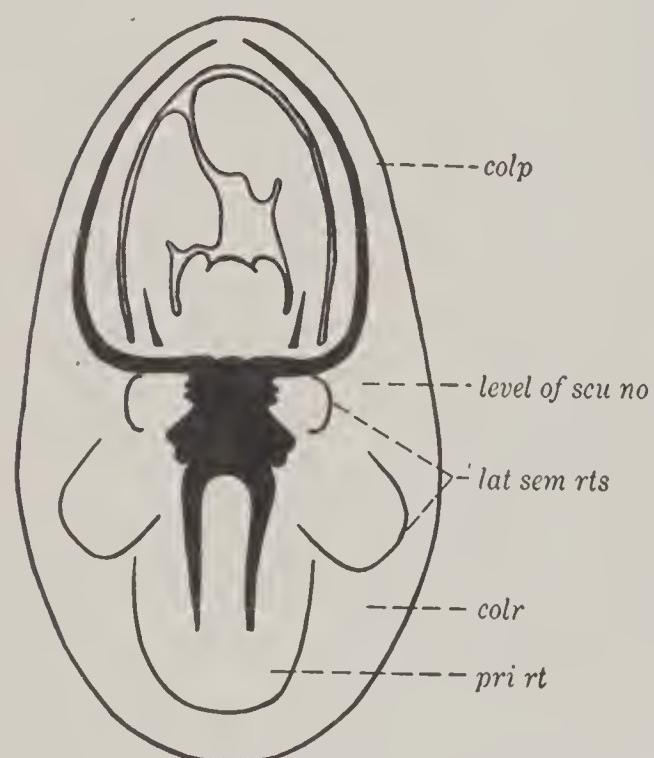


FIG. 65. Diagrammatic face view of the embryonic axis showing the procambial vascular system in black: *colp*, coleoptile; *colr*, coleorhiza; *lat sem rts*, lateral seminal roots; *pri rt*, primary root; *scu no*, scutellar node. (After Avery.)

embryo and the seedling axis of the grasses has occupied the attention of morphologists for over a century; and there has been no general agreement in the interpretation of the various parts of the embryo. This has resulted in a voluminous literature which is well summarized by Avery (1), McCall (9).

Percival (10) states that the view which "is most in agreement with the development and structure of the embryo of wheat is that which regards the scutellum, epiblast, coleoptile, and first green leaf as the first four leaves of the plant." McCall (9) interprets the epiblast "as a vestigial leaf," the scutellum as "the functional cotyledon, divergent from the second node" and

INTERPRETATION OF THE EMBRYO AND THE SEEDLING Axis.—

The structure of the

"the coleoptile as a third leaf." Avery (1) regards the scutellum as the cotyledon or first leaf of the plant, the coleoptile as the homologue of a foliage leaf or the second leaf, and the leaf distal to it as the third leaf. He states that "the epiblast, when present, cannot be considered a rudimentary cotyledon." More recently Boyd and Avery (3) reaffirmed this view, stating that "the coleoptile is the first leaf above the single cotyledon."

All of these investigators agree that the use of the term *mesocotyl*,

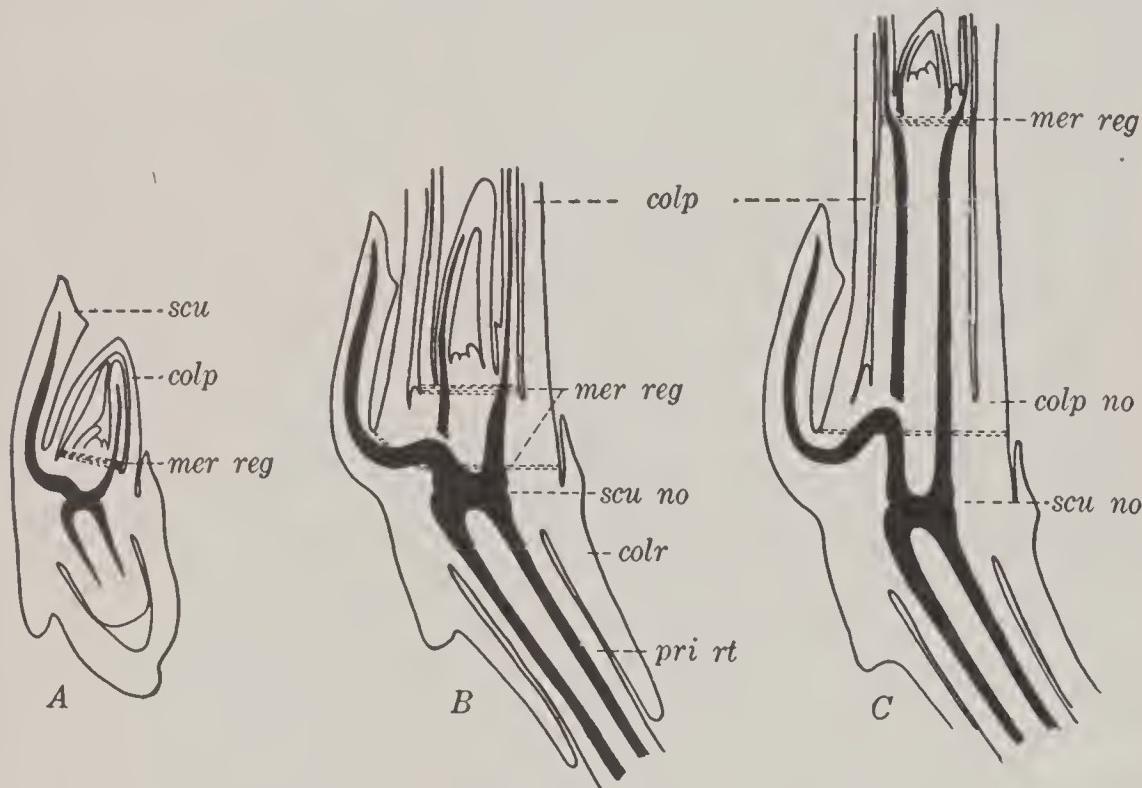


FIG. 66. *A*, median side longisection of dormant embryo; *B*, the same, 7 days old in which slight elongation of the axis above the scutellar node is taking place; *C*, the same, in a month-old plant showing the elongated second internode sheathed by the coleoptile. Meristematic regions of elongation are shown with dashes: *colp*, coleoptile; *colp no*, coleoptilar node; *colr*, coleorhiza; *mer reg*, meristematic region; *pri rt*, primary foot; *scu*, scutellum; *scu no*, scutellar node. (After Avery.)

as originally applied to the first internode, is misleading, since it implies that the first internode is a part of the cotyledon. While differences in terminology do not modify the actual structure, they do tend to create confusion in the literature; and it is desirable that a uniform nomenclature be applied to the embryo and seedling of the grasses.

GERMINATION. — In germination, the wrinkled surface of the pericarp over the embryo becomes smooth, and the entire wall is stretched. Following the rupture of the pericarp, the coleorhiza emerges, and the enlargement of the epiblast and other embryonic

structures extends the slit in the pericarp until the coleoptile is exposed. After the coleorhiza has elongated about a millimeter, the enclosed primary root digests and pushes its way through it. Shortly thereafter, the first pair of seminal roots emerges from the sides of the short hypocotyl, near the cotyledonary node; and these three roots grow with about equal rapidity until, at the end of two or three days, there is little difference in their length or thickness. (Figs. 58, 62.) At about this time, the second pair of seminal roots emerges above the first pair; and, in some cases, a sixth rootlet may develop behind the epiblast.

McCall (9) reports that he and Taylor observed that in most cases only three roots developed; but in a fairly large number of cases, four developed — the primary root, the first pair, and one of the second pair of seminal roots. In a smaller number, five roots developed; and, "as a rule, only relatively few seedlings of most varieties of wheat have the full potential complement of six seminal roots."

During the development of the seminal root system, the coleoptile elongates and the enclosed foliage leaves enlarge, the former protecting the leaf primordia and stem apex as they grow through the soil. The degree of emergence of the coleoptile is conditioned by depth of planting and environmental factors; and, after the tip of the coleoptile is above the soil surface, the first and second foliage leaves push through the small pore near its apex. Where wheat is sown at a depth of $1\frac{1}{2}$ to $2\frac{1}{2}$ inches, there is little elongation of the first internode. After several days, the second internode elongates until the third node, from which the first foliage leaf is diverged, is raised to the level of the soil surface or just below it. The bud in the axil of the coleoptile develops, and adventitious roots may arise from the internode above. At this time, elongation of the second internode ceases, and the roots which constitute the first whorl of the adventitious root system are formed.

Under average conditions the lower internodes, above the first whorl of adventitious roots, do not elongate much; and the production of roots at the nodes, together with the development of the axillary buds, results in the formation of several secondary axes or tillers and a fibrous secondary root system.

THE PRIMARY ROOT. — The primary root has an exarch, radial protostele with from seven to eleven protoxylem points. At a

level where maturation is complete, there are three well-defined regions: (1) the epidermis; (2) the cortical zone limited centripetally by the endodermis; and (3) the polyarch stele limited externally by the pericycle. (Fig. 67.)

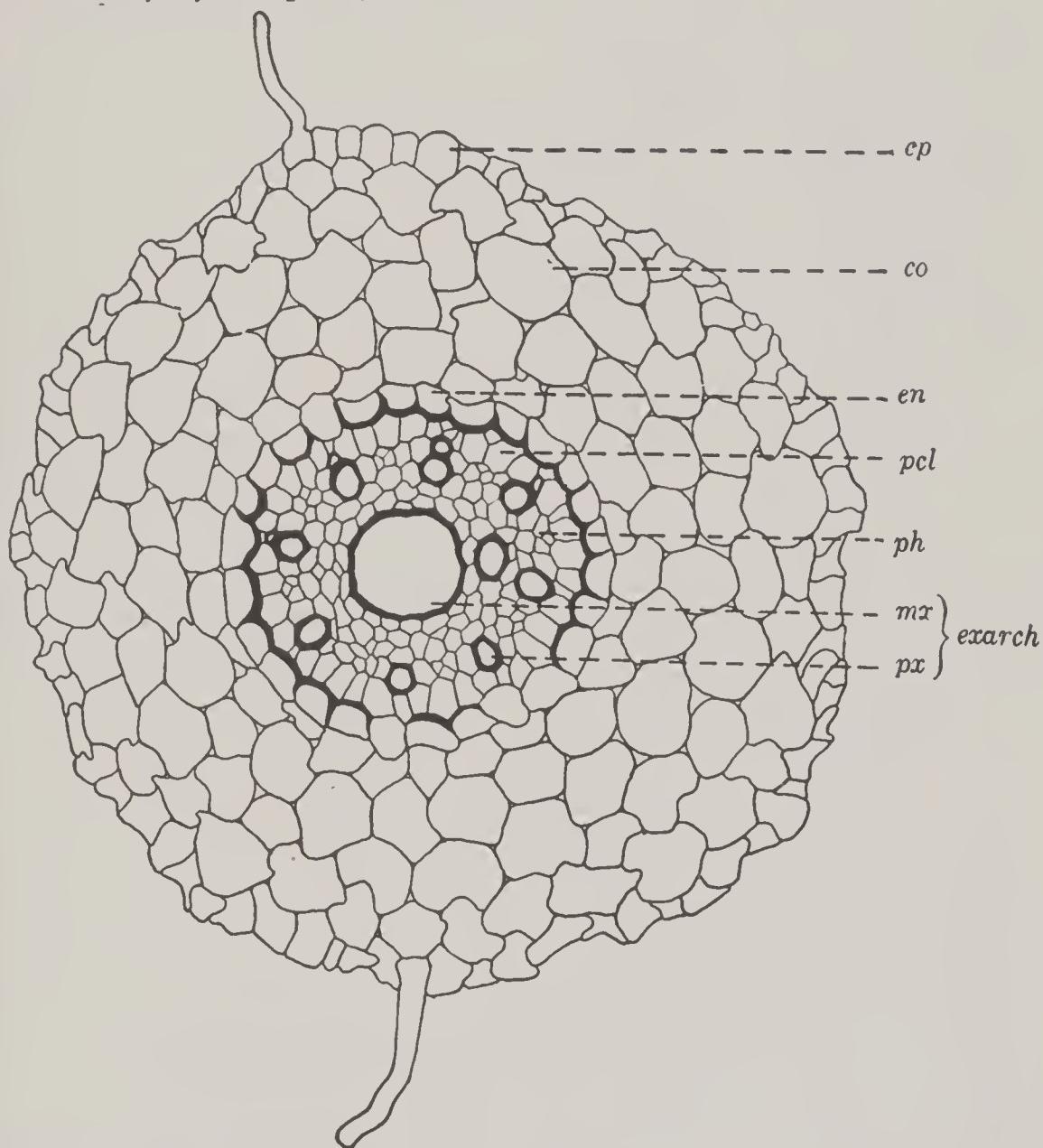


FIG. 67. Transection of primary root of the wheat seedling: *co*, cortex; *en*, endodermis; *ep*, epidermis; *mx*, metaxylem; *pcl*, pericycle; *ph*, phloem; *px*, protoxylem. (After Avery.)

The epidermis consists of thin-walled cells which are elongated in their axial dimension. Many of them develop as root hairs by an extension of a portion of the outer tangential wall, usually that part of it nearest the root tip; and they may reach a length of 1 to $1\frac{1}{2}$ mm. Ultimately they become desiccated, and the epidermis, with much of the cortical tissue, may disintegrate and die. The cortex consists of four to eight layers of rather compact

parenchymatous tissue with small intercellular spaces at the angles of the cells. The endodermis is thin-walled, except for the Casparyan strips; but, later in ontogeny, the radial, end, and inner tangential walls become much thickened, the latter ones appearing to be stratified.

The pericycle is single-layered, with cells of almost uniform size and dimension, except outside the protoxylem points, where they are smaller. As the root matures, and the cortical cells disintegrate, the walls of the pericyclic cells may become somewhat lignified and sclerotic. The protoxylem consists of a few small annular or spiral vessels; and centrad to them is a single large pitted metaxylem element. Alternate with the protoxylem strands are small groups of phloem cells, usually two to four in number; and between the phloem and xylem are fundamental parenchyma cells. When the epidermis and cortical tissues are finally shed, the stelar tissues remain functional, being protected by the thick-walled endodermal and pericyclic cells, as well as by the fundamental parenchyma, which also becomes thick-walled. The character of the phloem and xylem cells remains unchanged.

The ontogeny of the root is similar to that of corn, barley and other grasses in which the root meristem is differentiated into three histogens. The outermost one is the calyptrogen, from which the root cap is differentiated by successive periclinal divisions; and, since the peripheral layers of the root cap are successively abraded, it never becomes very massive. (Fig. 68.) The plerome gives rise to the stelar structures; and, between the plerome and calyptrogen, a single layer of meristematic cells produces the cortical and epidermal tissues. Periclinal divisions of the cells of this intermediate layer produce daughter cells, the outermost ones dividing only anticlinally to form the epidermis; while the inner daughter cells, by subsequent divisions in all planes, give rise to the cortical parenchyma and endodermis. The other seminal roots resemble the primary one in the essential details of structure and ontogeny.

The origin of lateral roots is pericyclic, occurring in sectors of this layer directly outside of the phloem groups and between two adjacent protoxylem strands. The pericycle becomes multi-layered by successive periclinal divisions, a conical mass of meristematic cells is formed, and the histogens develop which give rise to tissues as described for the primary root.

ADVENTITIOUS Roots. — The roots of the adventitious system arise in the intercalary meristems at the bases of the lower internodes of the culm, and differ from the seminal roots in certain

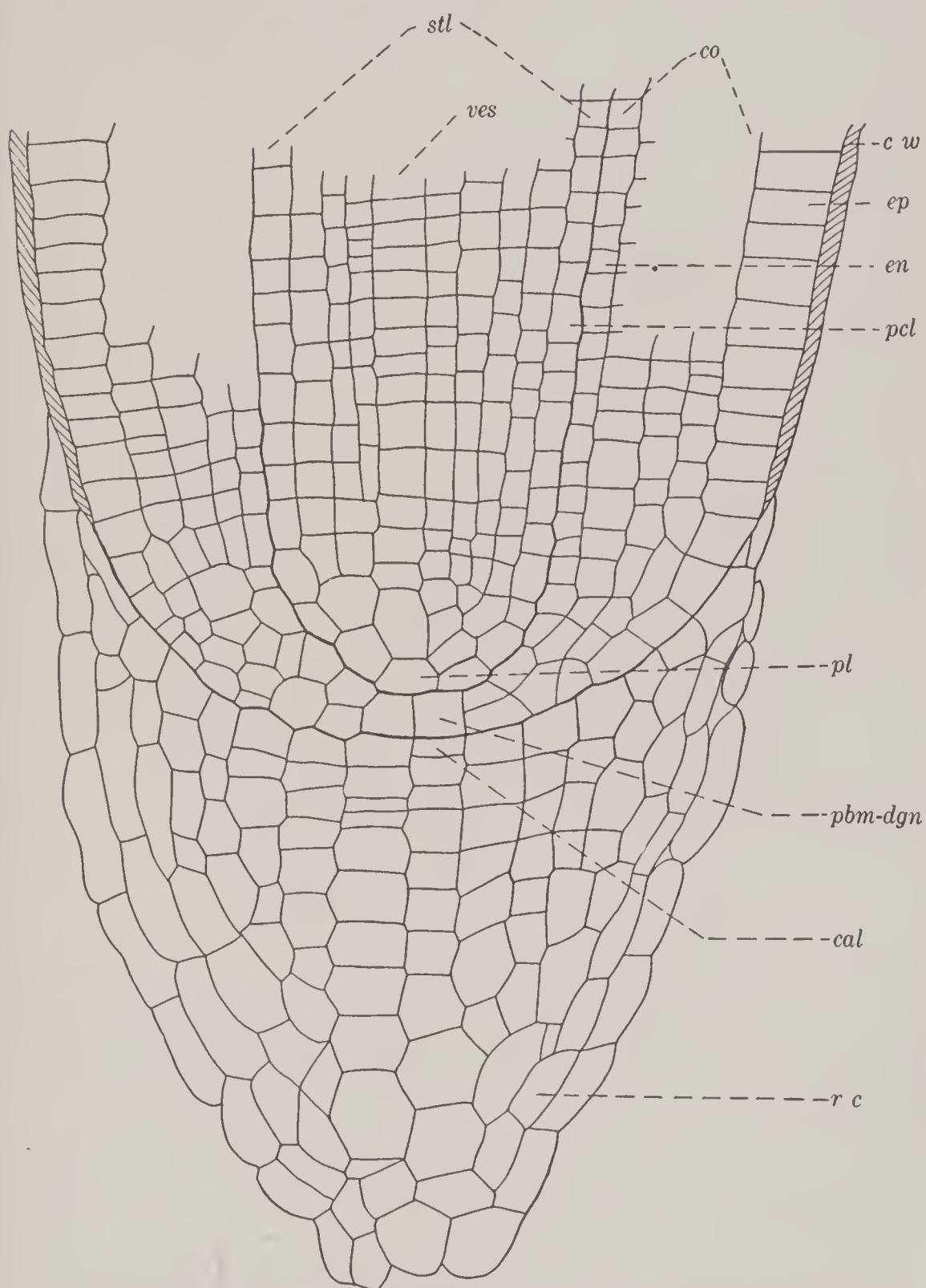


FIG. 68. Median longisection of tip of seminal root: *cal*, calyptrogen; *co*, cortex; *c w*, mucilaginous cell wall; *en*, endodermis; *ep*, epidermis; *pbm-dgn*, periblem-dermatogen; *pcl*, pericycle; *pl*, plerome; *rc*, root cap; *stl*, stele; *ves*, cells which become vessel segments. (Redrawn from Percival, *The Wheat Plant*, Duckworth and Co.)

respects. The cortical cells are more persistent; and there may be a hypodermal zone, two or three cells in thickness, which becomes sclerotic and protects the parenchymatous cells centrad to it. Percival (10) reports that in the stronger adventitious roots arising from aerial nodes, the cortical cells frequently have chloro-

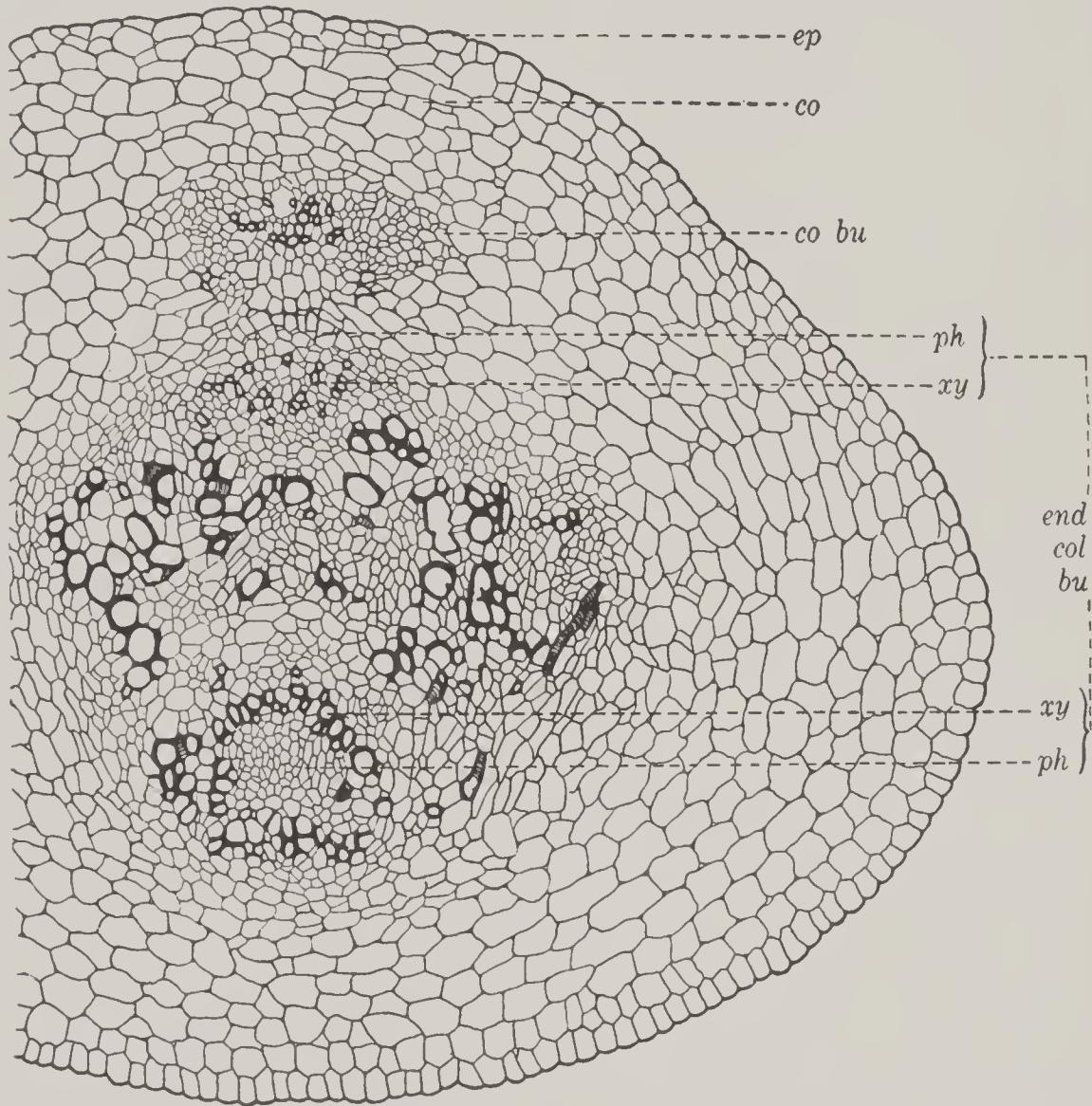


FIG. 69. Transection of the lower portion of the first internode of a four weeks old plant : *co*, cortex; *co bu*, cortical bundle; *end col bu*, endarch collateral bundles; *ep*, epidermis; *ph*, phloem; *xy*, xylem. (After Avery.)

plasts so that the stele appears to be surrounded by a zone of chlorophyllose tissue. Other differences in the stele are the development of several large metaxylem vessels instead of a single one; and the presence of a correspondingly smaller amount of stelar parenchyma which becomes lignified early in ontogeny so that it is difficult to distinguish protoxylem from parenchyma in transections.

ANATOMY OF THE TRANSITION REGION — FIRST AND SECOND INTERNODES. — In the first internode, the arrangement of the xylem, phloem, and parenchymatous tissue is transitional, lacking the definite arrangement found in the upper internodes. (Fig. 69.) There are two collateral bundles located on opposite sides of the stele; and the remaining xylem and phloem elements are arranged

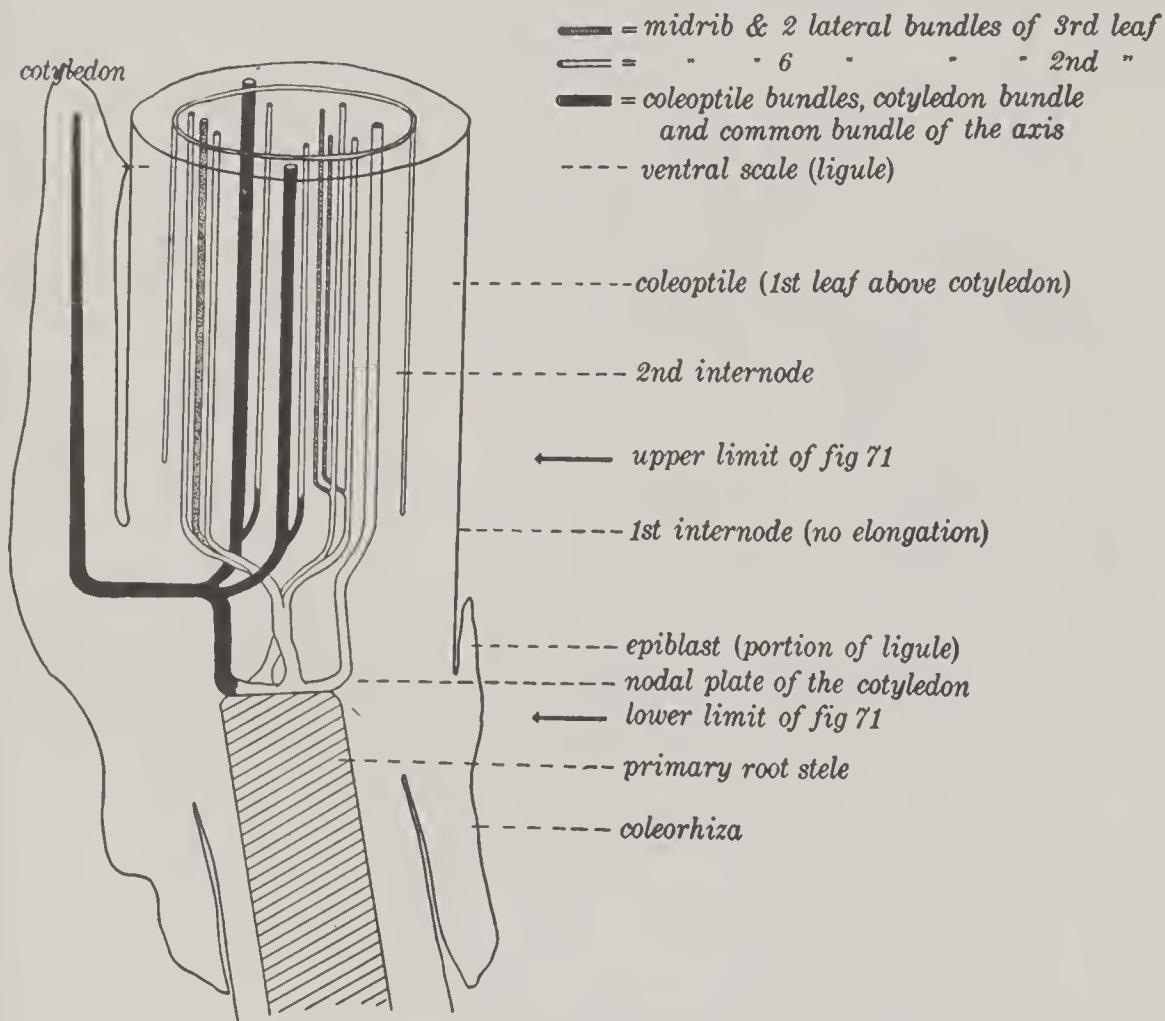


FIG. 70. Diagrammatic reconstruction of portion of seedling showing principal structures present, and vascular inter-relationships of cotyledon with axis, coleoptile, and first foliage leaf. Nodal plate of the cotyledon is main level at which vascular transition takes place and the first internode is also in part a transition region. (After Boyd and Avery.)

in an irregular fashion, the xylem being exarch, endarch, or indefinite in its orientation. The scutellar bundle occupies a cortical position, but the stele and cortex are not limited by a distinct pericycle and endodermis respectively.

The vascular system of the transition region has been described by Boyd and Avery (3) as consisting of four groups: (1) A bundle connecting the midrib of the second leaf to the cotyledonary plate. (2) The traces of the scutellum, coleoptile and second

leaf. These are connected on the scutellar side of the axis with a "common" bundle, that extends through the stem for some dis-

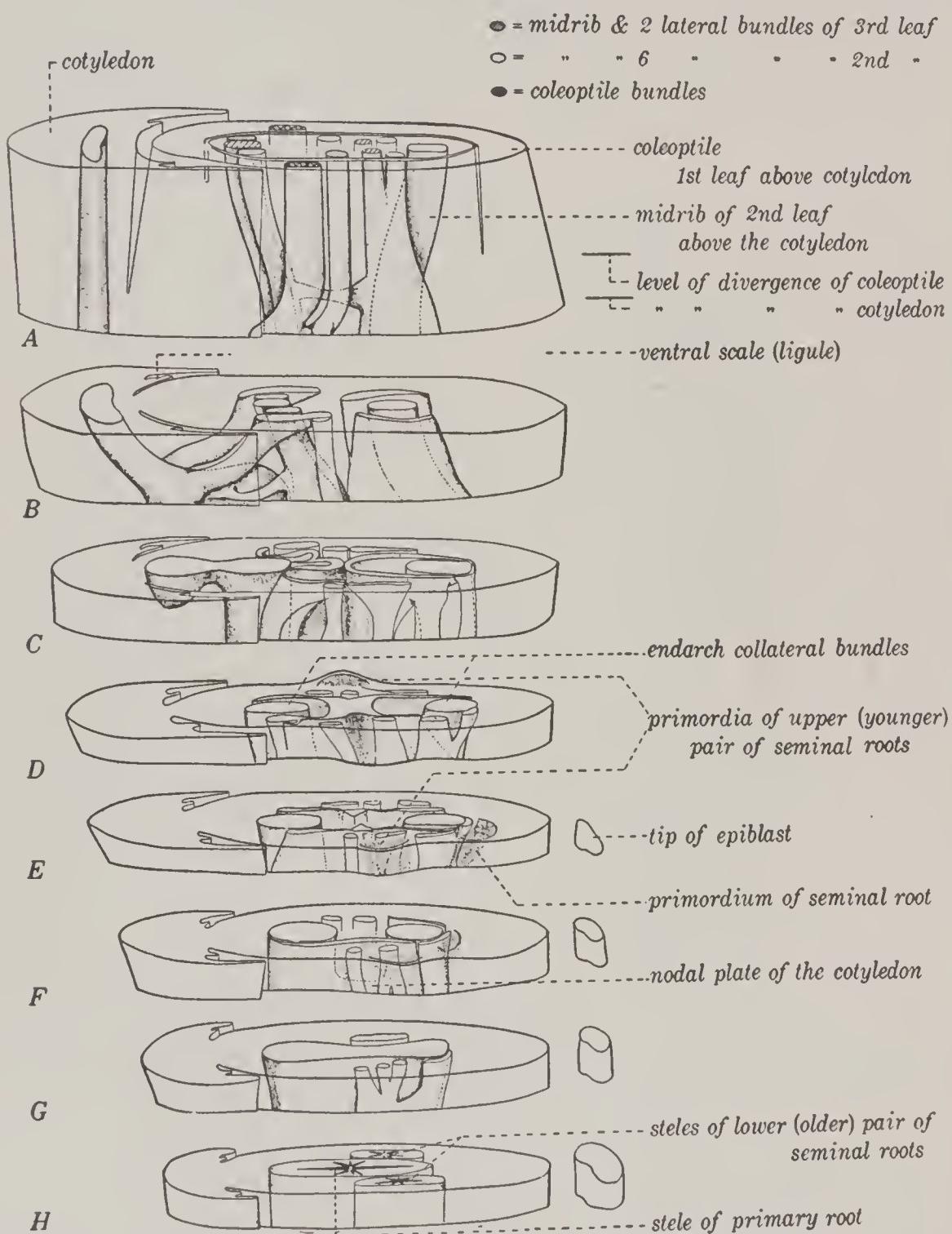


FIG. 71. Detailed course of vascular bundles and scattered vascular elements in portion of seedling, upper and lower limits of which are indicated in Fig. 70. (After Boyd and Avery.)

tance and terminates as a leaf trace or traces. The median lateral bundles of the second leaf are united with adjacent coleoptilar bundles, and the resultant bundles anastomose with the scutellar

bundle. In this manner, the common bundle is formed which extends to the cotyledonary plate where it is united with the bundle from the midrib of the second leaf. (3) The remaining four lateral bundles of the second leaf and two lateral bundles of the third leaf; and (4) the vascular elements of the seminal roots which anastomose with the bundles of the second leaf and are connected

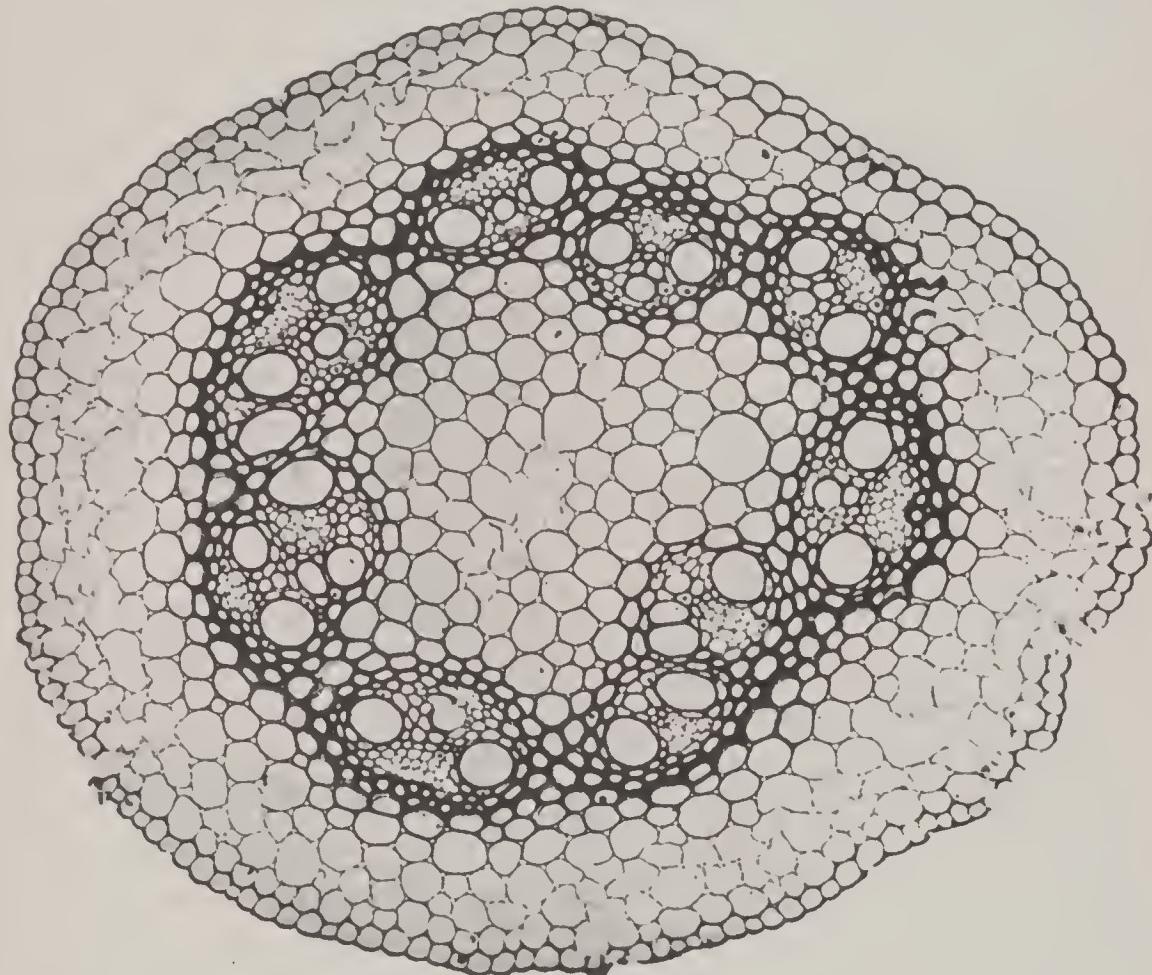


FIG. 72. A transection of the second internode of young wheat plant.

indirectly with the lateral bundles of the third leaf. (Figs. 70 and 71.)

The second internode, which extends from the point of divergence of the coleoptile to the first foliage leaf above, is less transitional in character than the first internode. It resembles the higher internodes except that the bundles are not as clearly defined, and there are some strands in which the differentiation of the xylem is intermediate between the exarch and the endarch arrangement. (Fig. 72.)

THE ANATOMY OF THE STEM. — In most wheats, the culm is subterete, hollow in the internodal regions and solid at the constricted

nodes where the vascular bundles form a lignified diaphragm. There are five principal tissue systems: (1) epidermis, (2) mechanical tissue, (3) chlorophyll parenchyma, (4) fundamental parenchyma, and (5) vascular bundles. (Fig. 73; see also Fig. 24.)

Aside from the guard cells of the stomata, there are two types of epidermal cells, one of which is narrow and elongated, the other short and isodiametric. The elongated cells are arranged

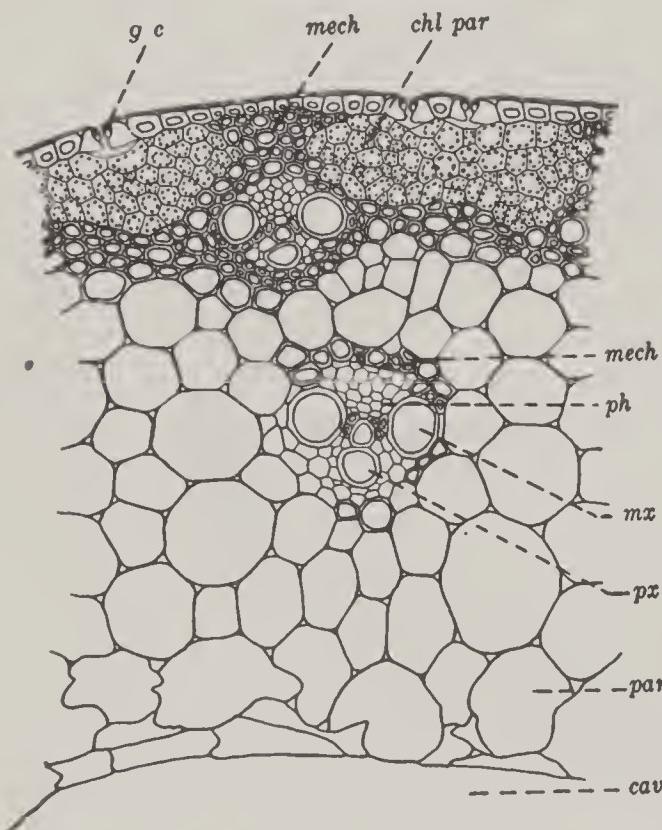


FIG. 73. A transection of a sector of the stem: *cav*, central cavity of the stem; *chl par*, chlorophyll parenchyma; *g c*, guard cells; *mech*, mechanical tissue; *mx*, metaxylem; *par*, parenchyma; *ph*, phloem; *px*, protoxylem.

in longitudinal rows, separated at intervals by the smaller cubical ones; and the width of the cells varies, those which adjoin the mechanical tissue of the hypodermis being narrower than those outside the chlorenchyma. The walls are much thickened and there is a well-developed cuticle on the portions which are not covered by the leaf sheath. The stomata occur in single or double rows and are similar to those found in the leaf. In varieties in which the stem is grooved, there may be short scabrous hairs developed along the furrows.

The mechanical tissue of the hypodermal region is made up of elongated, fibrous cells with thick walls and narrow lumina, which form a continuous zone of variable thickness within the epidermis; and this encloses the longitudinal bands of chlorenchyma, as well as the smaller peripheral bundles of the vascular system. (Fig. 74, A.) The chlorenchyma abuts the epidermis directly, consisting of thin-walled cells that are circular in transection, elongated in the axial dimension with somewhat sinuous longitudinal walls. The rows of stomata are so located that the substomatal cavities open into the parallel bands of chlorenchyma. These are frequently arranged in pairs and adjacent bands may

be united, forming broader ones. They are wide at the upper limits of the internode, taper gradually, becoming much narrower beneath, and finally disappear entirely near the base of the internode. Percival (10) has noted that the width of the individual bands of chlorenchyma is greatest in the upper internodes, and that they are also more closely grouped so that the upper part of the culm has a uniform green tint. In the three lowest internodes, there is less chlorenchyma, and it occurs chiefly in the upper part of each, being reduced or entirely wanting at the bases.

The fundamental parenchyma extends from the zone of mechanical tissue to the central cavity. It consists of thin-walled cells that are polygonal in transection and elongated in the longitudinal dimension, with those adjacent to the mechanical tissue being longer than the centrally located ones. The cells may become lignified in the lower internodes, and parenchymatous cells which have become thick-walled also constitute a part of the solid diaphragm at the nodes.

The vascular tissue in the internodal region consists of two rings of bundles. The outer ring consists of small bundles that alternate with bands of chlorenchyma, while the larger bundles of the inner ring lie in the fundamental parenchyma. (Fig. 73.) The endarch, collateral bundles are surrounded by a sheath of mechanical tissue consisting of slender elongated fibers; but, in the case of the smaller bundles which are embedded in the hypodermis, the fibers of the sheath cannot be differentiated from those of the adjacent tissue. The protoxylem consists of one or two annular or spiral vessels; and, in some cases, the innermost element is reinforced with a combination of rings and spiral thickenings. The large, laterally placed, metaxylem vessels are pitted and between them are several small pitted tracheids. The phloem is comprised of slender thin-walled sieve tubes and companion cells. (Fig. 74, *A* and *B*.)

THE COURSE OF THE BUNDLES IN THE STEM. — At each node, some 25 to 35 bundles enter the stem from the leaf sheath. About half of these pass through the node into the outer hypodermal ring, while the remaining somewhat larger bundles penetrate more deeply and become a part of the inner vascular ring. The parallel bundles follow a vertical course through the internode to the next lower node, where there are anastomoses, branchings, and changes

in the course of the bundles which, together with the entrance of additional bundles from the leaf, result in the formation of the nodal plate. Percival (10) has observed that, in most cases, the hypodermal bundles extend through a single internode, anastomosing with other bundles at the first node below. The number of bundles in the inner ring is reduced by anastomoses to about one-half their original number as they pass through the second

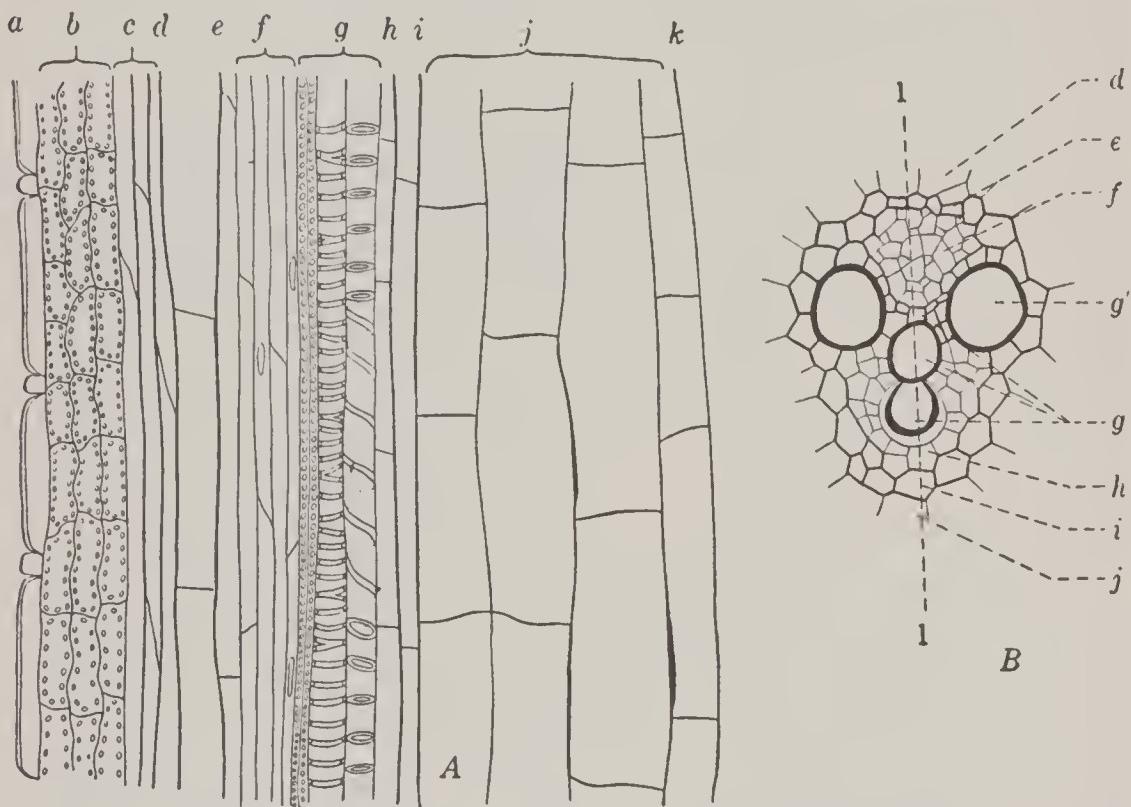


FIG. 74. A, longisection of a portion of the stem from epidermis to lacuna. The plane of the section with respect to the vascular bundle is indicated by the dotted line 1-1 in B. B, transection of a mature stem bundle: a, the epidermis showing two types of epidermal cells; b, chlorenchyma; c, mechanical tissue centrad to the chlorenchyma; d, parenchyma; e and i, mechanical tissue of the bundle sheath; f, phloem; g, primary xylem elements consisting of a pitted tracheid, spiral vessel, and an annular or annular-spiral vessel; g', metaxylem vessel, not shown in A; h, xylem parenchyma surrounding protoxylem elements; j, parenchyma; k, margin of the central lacuna.

internode. Thus, in any given internode, one-half of the large bundles can be traced to the leaf that is diverged at the node immediately above; and the remainder to the leaf diverged from the second node.

In the nodal region, the bundles are surrounded by a sheath of chlorenchyma, and differ from the internodal bundles in the number and character of the xylem elements. In general, the xylem elements are short, pitted or reticulate tracheids; and the bundles may be amphivasal rather than collateral.

ANATOMY OF THE LEAVES — THE COLEOPTILE. — The coleoptile, or second leaf, consists of a parenchymatous cylinder, limited outwardly and inwardly by epidermal tissue, through which two vascular bundles extend. The thin-walled cells of the outer epidermis are elongated, and there are one or two rows of stomata, lying parallel to the vascular strands, that pass from the base to approximately the tip of the leaf where the stomata are more

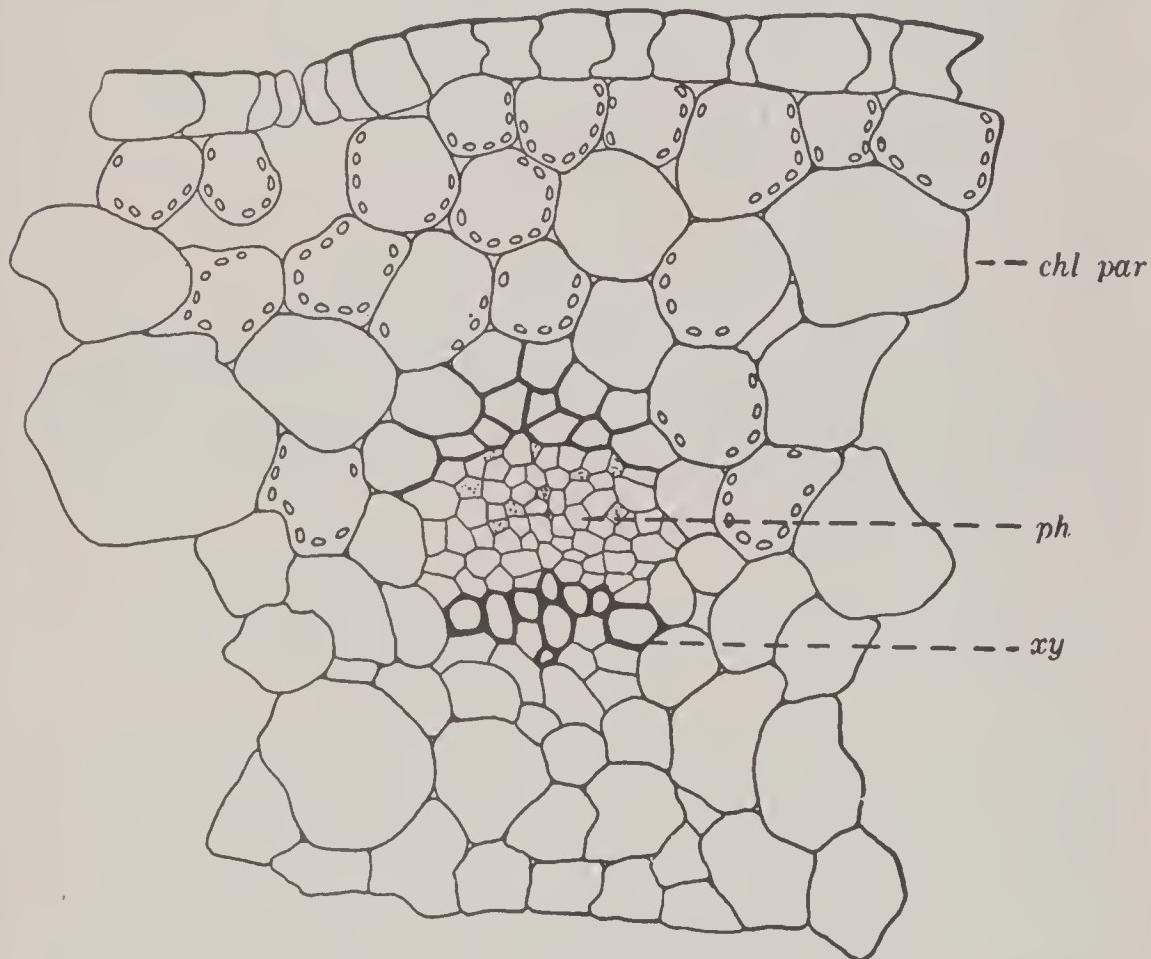


FIG. 75. Transection of a small portion of the coleoptile including the vascular bundle and surrounding tissue: *chl par*, chlorenchyma; *ph*, phloem; *xy*, xylem. (After Avery.)

numerous. No hairs are developed on either epidermis, and the inner one has no stomata. The parenchymatous cells abutting the outer epidermis and the cells surrounding the vascular bundles contain chloroplasts. (Fig. 75.) The vascular bundles are collateral; and, as compared with the stem bundles, have relatively more phloem than xylem.

THE PROPHYLLS. — The structure of the prophyll is not unlike that of the coleoptile. The rectangular epidermal cells are elongated and there are unicellular hairs along the margins of the flat surface of the prophyll. At its apex, longitudinal rows of

stomata lie parallel to, and on either side of, the bundles. The parenchymatous cells of the mesophyll do not contain chloroplasts except in the apical region and adjacent to the bundles. Two large bundles are located in the angles of the prophyll where the convex and flat sides meet, and the convex portion is traversed by several smaller ones. The margins of the leaf are strengthened by strands of mechanical tissue, and there may be a few supporting cells abutting the smaller vascular bundles.

THE FOLIAGE LEAVES. — The structure of the foliage leaf is more complex than that of the coleoptile and prophylls. The epidermal cells are arranged in rows which run parallel to the long axis of the blade; and, as in the stem, some of these are elongated while others are approximately square in surface view. The elongated cells, may form continuous rows, or they may be separated at intervals by the short cells; and they also occur between the longitudinal rows of stomata. Epidermal hairs, when present, are of varying lengths and arise from the surface in a more or less regular arrangement.

The adaxial surface is somewhat ridged, while the abaxial one is nearly flat; and in the furrows of the former are single or double lines of stomata with bands of motor or bulliform cells between them. (Fig. 76.) Each band is three to seven cells in width and the cells comprising it are thinner walled than the adjacent epidermal cells. The motor cells are shorter than the long cells of the epidermis; but, as seen in transection, are thicker than any of the other epidermal cells. Since their outer surfaces are not cutinized, they lose water under conditions which cause high transpiration, and the decreased turgidity results in an incurving of the adaxial surface of the blade. The number of stomata is greater on this surface than the abaxial one and the curling tends to decrease the amount of water loss. The stomatal apparatus consists of two narrow guard cells which surround the stoma, and two accessory cells. (Fig. 5.) The development of the stoma is similar to that described for *Zea*.

The abaxial epidermis is like the adaxial with respect to the arrangement of the cells, but differs from it in the absence of ridges and motor cells. In addition to this, the cell walls may be somewhat thicker, the number of hairs fewer, and the stomata more commonly occur in single rows. The abaxial epidermis of the sheath resembles that of the blade, with thick sinuous walls,

while the cells of the adaxial epidermis are thin-walled with few stomata.

The chlorenchyma of the mesophyll is very uniform, although the cells abutting both epidermal surfaces may be somewhat elongated in a manner suggesting palisade tissue. There are large intercellular spaces subtending the stomata and projecting into the central portion of the mesophyll. In the sheath, chlorenchyma strands, three or four cell layers in thickness, occur between the vascular bundles; and in the mature sheath, large lacunae develop centrad to them.

Vascular bundles of two sizes extend parallel with the long axis of the lamina, and small transverse veins interconnect the

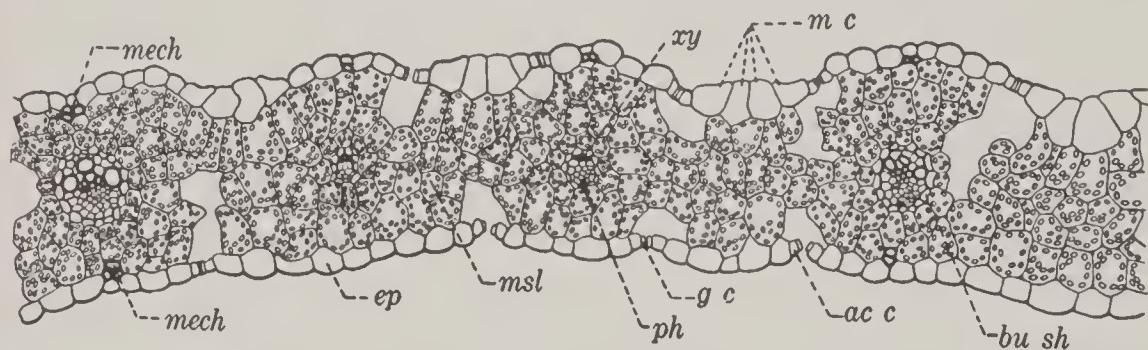


FIG. 76. Transection of small portion of foliage leaf: *ac c*, accessory cell; *bu sh*, bundle sheath; *ep*, epidermis; *g c*, guard cell; *m c*, motor cells; *mech*, mechanical tissue; *msl*, mesophyll; *ph*, phloem; *xy*, xylem. (After Avery.)

longitudinal strands which may occasionally branch, or anastomose toward the apex of the blade. All the bundles are collateral and the larger ones resemble those of the stem in their organization, having one or two annular or spiral elements and two large pitted vessels. The small longitudinal bundles have no large vessels, and the xylem of the transverse bundles usually consists of short tracheids. In all cases, phloem is present, but in the transverse bundles it is limited to a few somewhat elongated parenchymatous cells. The bundles are surrounded by a double sheath, the inner layer consisting of elongated thick-walled cells, and the outer of parenchymatous cells which are usually devoid of chloroplasts at maturity. In some cases, the outer layer of the sheath does not completely encircle the bundle, being restricted to a sector over its adaxial or xylem portion.

Longitudinal strands of thick-walled mechanical tissue are located above and below the bundles, and there is also a strand of this type extending along each margin of the leaf blade immedi-

ately within the epidermis. Those adjacent to the smaller bundles consist of a few fibers; but near the larger ones, the fibrous tissue is much more extensive. It may occupy the entire space between the bundle and the epidermal layers, so that a continuous band of sclerenchyma is formed, consisting of the fiber strands and the mechanical tissue of the inner layer of the bundle sheath. In the leaf sheath, the sclerenchyma is usually restricted to zones adjacent to the abaxial surface, the amount increasing toward the node; but there are a few mechanical elements abutting the adaxial one, except opposite the smaller bundles.

The ligule is a non-vascular emergence which arises at the junction of the blade and sheath. It is parenchymatous and is three or four cells in thickness at its base. The inner surface of the ligule is continuous with the epidermis of the leaf sheath, and both surfaces are without hairs or stomata. The free upper edge may be somewhat fringed, due to the elongation of its marginal cells.

THE ONTOGENY OF THE SHOOT. — The development of the growing point of the stem axis, and the differentiation of the leaves and axillary buds, have been investigated by Rösler (12). The peripheral layer of the bud meristem constitutes a dermatogen which divides only anticlinally, except at points where a leaf primordium is initiated. The leaf originates entirely from the dermatogen, the first evidence of primordial development being the periclinal division of a group of these cells. Rapid divisions of the derivative cells follow, and there is an early blocking off of the mesophyll region. The cells of the subepidermal layer, underlying the leaf primordium, also divide tangentially; but they contribute only to the development of the vascular system at the base of the leaf and the internode.

The formation of new buds or growing points involves the subepidermal tissues; and, according to Rösler, two different types of ontogeny may occur. In young plants, the tissue of the bud within the dermatogen may arise from a single subepidermal apical cell; or in some cases, from a plate of several subepidermal cells. This initial, or group of initials, forms the corpus of the axis, and by periclinal divisions two layers are produced. These are not exactly comparable to Hanstein's periblem and plerome, since the outer one gives rise to the cortex and the peripheral part of the stele, while the inner one differentiates the remainder

of the central portion of the axis. In older plants, there are two layers of initials within the dermatogen, one lying above the other. The outer one consists of a group of cells, the inner one of a single cell; and these differentiate the regions of the axis as in the first case. This type of development is found especially in the growing points of the floral region.

FLORAL DEVELOPMENT. — In the development of the flowers of a spikelet, the primordia of the bracts and the enclosed perfect, hypogynous flowers arise in acropetal succession. (Fig. 77, A.)

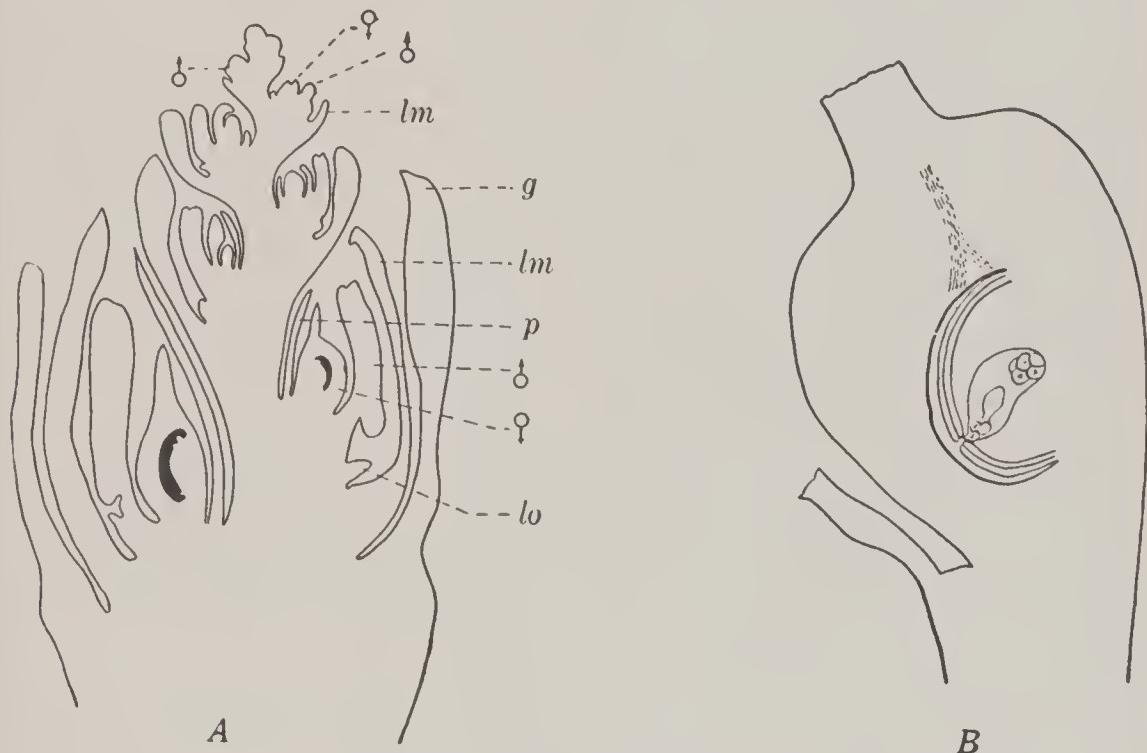


FIG. 77. A, median longisection of a young spikelet; B, longisection of the ovary showing the ovule with outer and inner integuments and the embryo sac: g, glume; lm, lemma; lo, lodicule; p, palea. The primordia of the stamens and carpels are indicated by the symbols ♂ and ♀ respectively. (Redrawn from Percival, *The Wheat Plant*, Duckworth and Co.)

Percival (10) has described the sequence and origin of the floral parts. In each flower, the lemma or flowering glume is the first structure to be differentiated, arising as a semicircular fold of tissue on the abaxial side of the meristematic tip with reference to the main axis of the spikelet. This is soon followed by three papillate, staminal primordia; and, shortly thereafter, the carpillary primordium arises as a crescentic ridge that partially surrounds the apex of the floral axis. At about this time, the primordia of the palea and lodicules appear, the latter arising from points on the axis somewhat lower than the point of origin of the staminal primordia.

In the differentiation of the carpel, the styles develop as two blunt conical outgrowths; and, coincident with this, the upper portion of the carpel grows over and encloses the rounded portion of the floral axis. In so doing, it forms a chamber in which the tip of the axis appears as a protuberance from the inner surface of the ovary; and it is at this point that the single ovule later arises.

MICROSPOROGENESIS. — The staminal primordia elongate rapidly and there is an early differentiation of a vascular strand in the meristematic tissue. An archesporial cell is formed in each angle of the anther, and this divides periclinally to form the primary parietal and inner sporogenous cells. Radial divisions of the parietal cell produce four cells; and these, with adjoining ones, form a parietal layer which encloses the sporogenous cell. Successive periclinal divisions of the cells of this layer result in three concentric, parietal layers, the inner one becoming the tapetum, and the outer, the endothecium. At first, the sporogenous cells form a single longitudinal row; but, later, radial and longitudinal divisions occur so that in transection there are about six radially arranged cells which function as pollen-mother cells. As the locules enlarge, the pollen-mother cells become spherical or oval and separate from one another, forming a single layer lining the anther chambers. Finally, meiotic divisions result in the formation of tetrads of microspores. The haploid number has been reported as eight for most varieties of wheat.

THE DEVELOPMENT OF THE OVULE. — The primordium of the ovule first appears as a hemispherical mass arising in a lateral position on the inner adaxial surface of the ovary from a broad placenta. (Fig. 77, B.) Percival (10) regards it as being derived "from the morphological apex of the floral axis," and states that its lateral position is "due to rapid growth of one side of the axis before the closure of the carpel." As the nucellar tissue increases, two integuments arise at its base, the inner one being formed at about the time that the archesporial cell is clearly differentiated, while the outer one begins to develop before the archesporial cell divides. (Fig. 78, B.) As growth of the nucellus and the integuments proceeds, the more rapid development of the latter results in the complete enclosure of the nucellus. (Fig. 78, C, D.) The outer integument never completely reaches the micropylar opening which is formed by the growth of the inner integument; and the former disintegrates before the maturation of the seed. The

unequal growth of the nucellus and its investing integuments results in the formation of a completely anatropous ovule.

MEGASPOROGÉNESIS AND THE MEGAGAMETOPHYTE. — The hypodermal archesporial cell is wedge-shaped, and successive divisions of it result in the formation of a linear tetrad of megasporangium mother cells. (Fig. 78, A-C.) The three outer cells disintegrate, and the innermost one enlarges greatly, functioning as the megasporangium. (Fig. 78, D.) The development of the megagametophyte proceeds

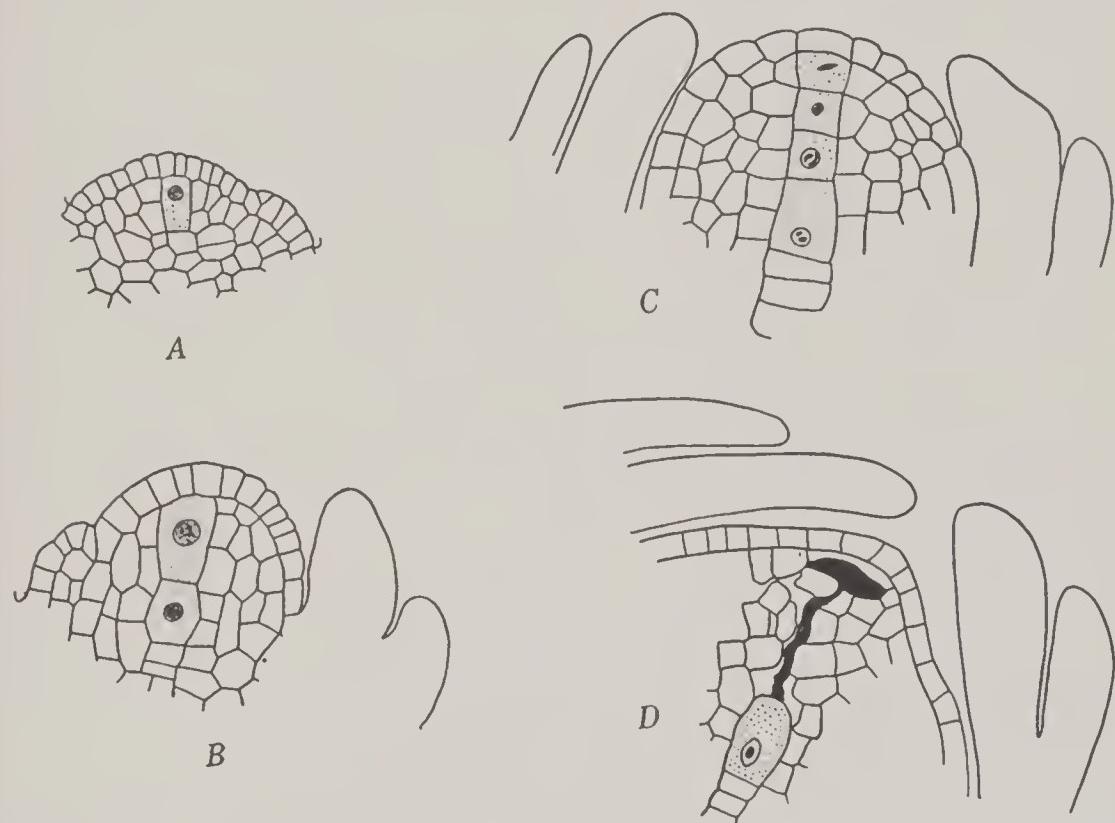


FIG. 78. A-D, median longisections of portions of young ovules: A, stage showing primary archesporial cell; B, after the first division of the archesporial cell; C, the tetrad stage; D, a later stage showing the collapse of the three outer cells. (Redrawn from Percival, *The Wheat Plant*, Duckworth and Co.)

to an eight-celled stage, during which time it increases in size and absorbs some of the nucellar tissue. The two synergids and the megagamete occupy the micropylar end of the megagametophyte; and, prior to gametic union, the polar nuclei fuse. The three antipodal cells increase in size and divide, the number ultimately produced varying from six to ten according to Percival (10), although Körnicke (7) suggests that 36 or more may be formed.

Brenchley (4) states that double fertilization occurs between 24 and 48 hours after pollination; and, although there may be some doubt as to a union of the primary endosperm nucleus with

the second microgamete in all cases in *Triticum vulgare*, Sax (13) observed the phenomenon in *Triticum durum*. It is possible that the fusion of the polar nuclei with the second microgamete may take place so rapidly that this stage is difficult to observe. The antipodal cells show signs of disintegration at the time of fertilization; and, as the embryo and endosperm develop, the surrounding nucellar tissue is also gradually resorbed. The outermost layer of the nucellus persists as an actively dividing tissue for some time, but ultimately its cells become disorganized and the radial walls are broken down. In the mature grain, it may appear as a crushed layer outside the aleurone cells of the endosperm.

EMBRYOGENY. — In the development of the embryo, the first division of the zygote is transverse, and the large, basal, daughter cell functions as the suspensor which does not divide again. The upper cell forms the embryo, dividing first in the transverse plane, and then a vertical wall is formed in both the cells so that the pro-embryo consists of four cells with a basal suspensor. Further divisions in all planes result in a marked increase in the size of the embryo; and, in a few days, the dermatogen can be distinguished surrounding a central body of cells.

At this time, the embryo is club-shaped with an elongated base, and the first form change occurs in the development of a lateral notch indicating the position of the growing point of the axis which appears on the side of the embryo away from the endosperm. (Fig. 79, B.) The distal portion of the embryo becomes the cotyledon or scutellum, which Percival regards as a terminal structure. A more generally accepted interpretation is that the growing point is terminal and the cotyledon a lateral structure; which, because of the slow growth of the apex and the rapid growth of the cotyledon, appears to occupy a terminal position. The position of the suspensor at the base of the axis, rather than at the lower portion of the cotyledon, supports the latter view.

Shortly after the apical meristem of the stem is defined, the primordium of the coleoptile arises as a fold of tissue surrounding the stem tip and forms a cone-shaped structure which encloses the primordia of the first foliage leaves. (Fig. 79, C, D.) At this time, the epiblast arises as a lateral outgrowth in the region of the cotyledonary node. There is intercalary growth at the base of the upper portion of the scutellum which elongates the apex, resulting in the formation of the overhanging ventral scale; and the develop-

ment of the epithelial layer occurs after this elongation has taken place. (Fig. 79, *F*, *G*.)

The differentiation of the primary root within the coleorhiza, or root sheath, takes place at about the time that the coleoptile begins to develop; and the histogens and root cap are clearly defined before the embryo is a millimeter in length. A difference in the growth rate of the cells of the root cap and those of the adjacent tissues results in the formation of a schizogenous cavity around the

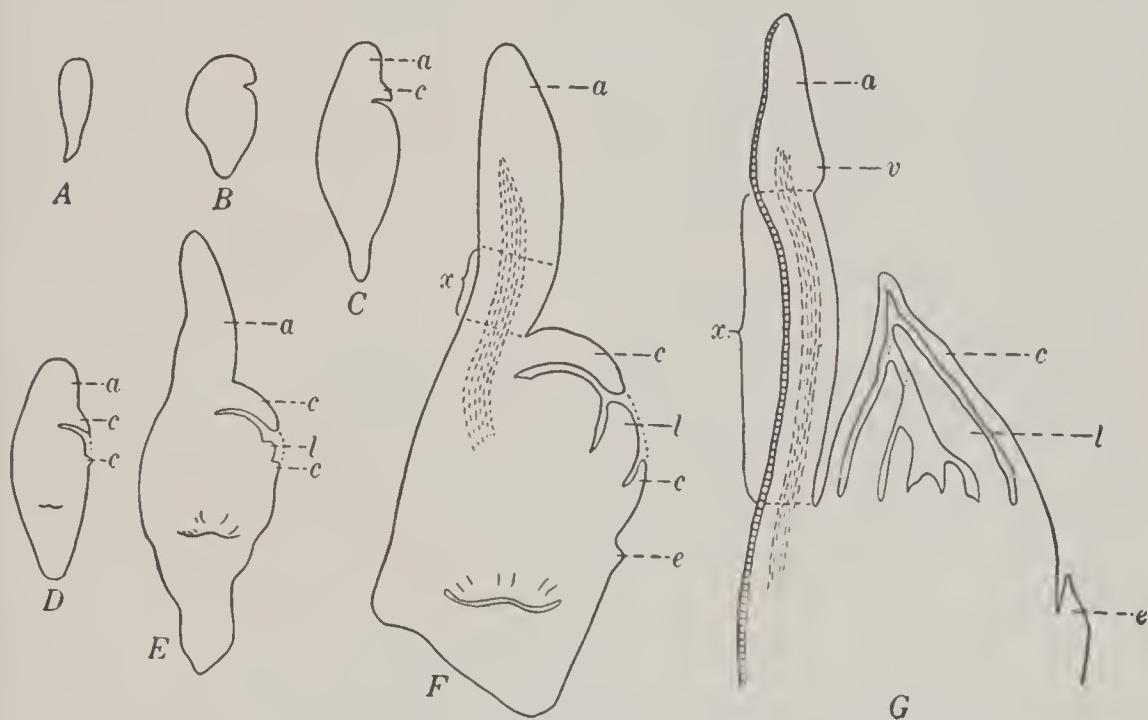


FIG. 79. *A-F*, longisections of embryos in progressive stages of development; *G*, epicotyledonary portion of embryo: *a*, upper portion of scutellum; *c*, coleoptile; *e*, epiblast; *l*, first foliage leaf; *v*, ventral scale; *x*, region of intercalary elongation of scutellum. (Redrawn from Percival, *The Wheat Plant*, Duckworth and Co.)

root apex. As the elongation of the embryonic root proceeds, this cavity is extended so that in the mature embryo the root is separated from the coleorhiza by a cylindrical cavity.

THE ENDOSPERM. — After fertilization, the development of the endosperm parallels that of the embryo; and, before the first division of the zygote, the primary endosperm nucleus undergoes division followed by a series of free nuclear divisions until considerable numbers of nuclei are formed. These occupy a parietal position in the embryo sac; and, by the time the embryo has reached the 10- to 15-celled stage, there is a continuous layer of endosperm cells lining the embryo sac. In six or seven days, the sac is completely filled with endosperm tissue which has developed

centripetally. The initial development of the endosperm occurs at the expense of the antipodal cells and the surrounding nucellar tissue, some of which is absorbed.

Brenchley (4) has investigated the development of the endosperm and points out that the differentiation of the cells on the ventral side opposite the furrow results in the formation of a peripheral layer of aleurone cells. The deposition of starch begins at about the tenth to eleventh day, when the endosperm cells are completely formed, and proceeds for five or six weeks until the conclusion of the ripening period. Starch is deposited first on the flanks of the endosperm, and none can be detected on the portion of the endosperm beneath the furrow connecting the two flanks until later in ontogeny. Finally, the cells become so filled with starch that the nuclei and cytoplasm of the cells are affected, and in those which contain large amounts of starch, the protoplasmic contents and the nuclei become disorganized.

THE INTEGUMENTS. — While the embryo and endosperm are undergoing progressive development and change, the two integuments are also being modified. Initially, each integument consists of two cell layers; but at about the time that the zygote divides, the cells of the outer one begin to disintegrate. This is evidenced in a loss of turgidity and a degeneration of the protoplasts; until, finally, the cell contents disappear completely and the cell walls are crushed and obliterated. (Fig. 80, A, B, C.) The inner integument retains its form, and its cells remain distinct, increasing in size until about the milk-ripe stage, when there is a collapse of the cells of the outer layer of the inner integument owing to a loss of cell contents. The cells of the inner layer of the inner integument persist for some time longer and in them are the pigments which give color to the yellow and red grained wheats. Finally, as the grain dries and shrinks in ripening, the radial walls of the inner layer become crushed and partially dissolved, so that the collapsed remains of the outer and inner walls represent all that is left of the seed coat at maturity. (Fig. 80, D.)

THE PERICARP. — The pericarp or ovary wall keeps pace with the development of the enclosed ovule. It consists chiefly of parenchymatous cells which lie between an outer and inner epidermis. As maturation proceeds, there is some differentiation and the cells of its outer epidermis begin to exhibit the pits and beaded thickenings described for the mature grain. The parenchyma is

colorless except for a chlorophyllose region one cell in thickness, adjacent to the inner epidermis; but there may also be chloroplasts in the subepidermal cells along the furrowed portion of the young pericarp. As maturity approaches, the cells of the inner epidermis fail to keep pace with the growth of the adjacent cells and become separated, forming the characteristic tube cells of the ripe pericarp.

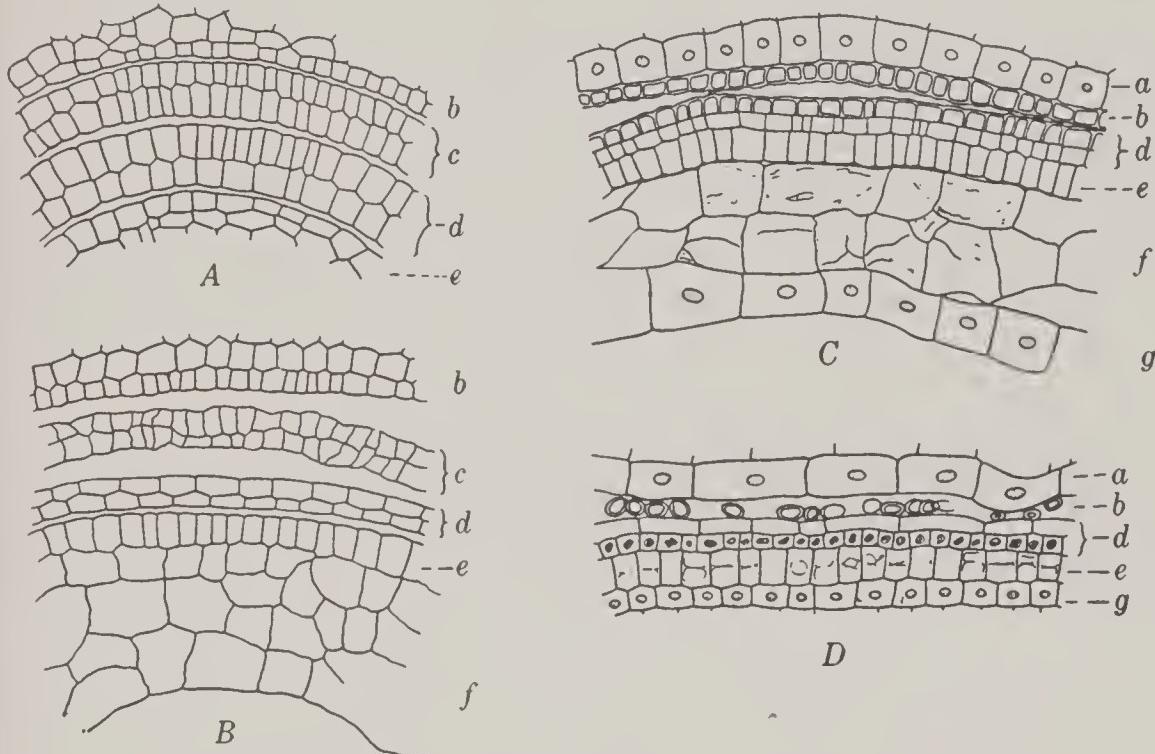


FIG. 80. A-D, transections showing the developmental changes occurring in the pericarp, integuments, and nucellus during the maturation of the grain: *a*, the cross cells of the pericarp; *b*, inner epidermis of pericarp; *c*, outer integument of ovule; *d*, inner integument of ovule; *e*, outer layer of nucellus; *f*, cells of nucellus; *g*, aleurone layer. (Redrawn from Percival, *The Wheat Plant*, Duckworth and Co.)

Shrinkage and desiccation cause a compression of the cells which come into intimate contact with those of the testa and in this manner the combined fruit-seed coat of the caryopsis is formed.

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CHAPTER VII

LILIACEAE

ALLIUM CEPA

ALLIUM and Asparagus are important genera in the lily family, and there are many ornamental plants in this group, including species of *Lilium*, *Tulipa*, and *Hyacinthus*. In the genus Allium, there are a number of strong-scented, pungent herbs characterized by the development of a scapose stem which, with the leaf bases, forms a bulb that may be small as in chives (*Allium Schoenoprasum* L.), or very well developed as in the common onion (*A. Cepa* L.). Other widely cultivated species are: *A. sativum* L., garlic; *A. ascalonicum* L., shallot; and *A. Porrum* L., leek, in which a pronounced bulb is nearly always absent.

GENERAL MORPHOLOGY

THE ROOT SYSTEM. — The root system is relatively shallow and fibrous. New cycles of adventitious roots continue to arise from the stem throughout the life of the plant, which radiate in all directions but do not penetrate the soil to any great depth. Sideris (16) reports that

"onion plants grown in water or in soil cultures produce two sets of roots from the time of their germination to the completion of their life cycle. The first set is produced at the time of germination and functions during the period between germination and formation of the bulb. . . . The second set is produced at the time of formation of the bulb and later, and functions during the period between the formation of the bulb and the death of the plant."

Thompson (19) finds that the roots of onion seedlings attain a depth of 2 inches and a lateral spread of 3 inches within 25 days after being planted; while in plants 12 inches tall with a base the size of a lead pencil, the roots reach a depth of 4 inches. At maturity, the majority of the roots are within 6 to 8 inches of the soil surface and the greatest penetration does not exceed 20 inches.

THE SHOOT. — The plant has a biennial habit, although it may persist vegetatively as a perennial by means of bulbs. The subterranean stem is a short, subconical structure from which the linear leaves are diverged in a $\frac{1}{2}$ phyllotaxy. It produces a long, hollow, leafless stem which arises from the terminal bud of the



FIG. 81. Basal portion of onion showing the bulb, the two-ranked arrangement of leaves, the manner in which the leaf sheaths enclose younger leaves, and the adventitious roots. (Photograph by J. Horace McFarland Co.)

underground axis and bears the inflorescence at its apex. In some instances, lateral buds from the axils of the fleshy leaves of the bulb may develop into flower stalks and produce terminal inflorescences.

The leaves arise from the short crown stem in a compact series, and the sheaths of the outermost, older leaves enclose the younger ones. The sheathing base of each leaf completely encircles the stem, and it is the development of the fleshy leaf bases, together with the absence of internodal elongation, that results in the for-

mation of the bulb of commerce. (Fig. 81.) The inner leaves emerge through the outer ones by way of a lateral slit at the apex of each leaf base. The linear blade is parallel-veined and cylindrical, with a hollow center at maturity. This is not continuous with the hollow formed by the circular leaf base, but is the result of a splitting away and disintegration of the centrally located parenchymatous tissue.

THE INFLORESCENCE AND FLOWER. — The inflorescence is a terminal umbel that is borne on an elongated flower stalk which reaches an average height of 3 or 4 feet, but may occasionally approach 6 feet. It is subtended by a papery spathe consisting of two or sometimes three bracts which enclose the umbel until it is split by the development of the first flowers. (Fig. 82, A.) The number of flowers in an umbel ranges from as few as 50 to over 1000. The pedicels which bear the individual flowers are usually long and slender, but may be short and rigid. The flower buds do not develop in regular centripetal or centrifugal order; and, consequently, flowers in various stages of development occur throughout the umbel.

The white or bluish flowers are regular and pentacyclic, consisting of a perianth of six similar parts arranged in two whorls, six stamens inserted at the base of the perianth segments in two cycles, and a pistil of three undiverged carpels. (Fig. 82, E, G.) The nectaries occur in the axils of the three inner stamens. The ovary is superior and there is a single, thin persistent style with a slightly three-lobed stigma. The anthers of the inner whorl of stamens dehisce before those of the outer, and both sets do so before the stigma is receptive. For this reason, cross-pollination is the rule and is effected through the agency of insects, although interpollination between flowers of the same umbel is undoubtedly a frequent occurrence.

ANATOMY

THE FRUIT AND SEED. — The fruit is a three-lobed, three-celled capsule, each valve or locule containing one or two black seeds at maturity, and the dehiscence of the fruit is loculicidal. Sachs (15) has described the seed, and the development of the seedling has been outlined by Anderson (1) and Hoffman (7). Kondo (11) investigated the structure of the seed coats of several species of *Allium* and found them to be similar in all major details.

In *Allium Cepa*, the thick-walled epidermal cells are filled with a very dark brown pigment; and the parenchymatous layer is similarly colored, consisting of six rows of thin-walled cells that

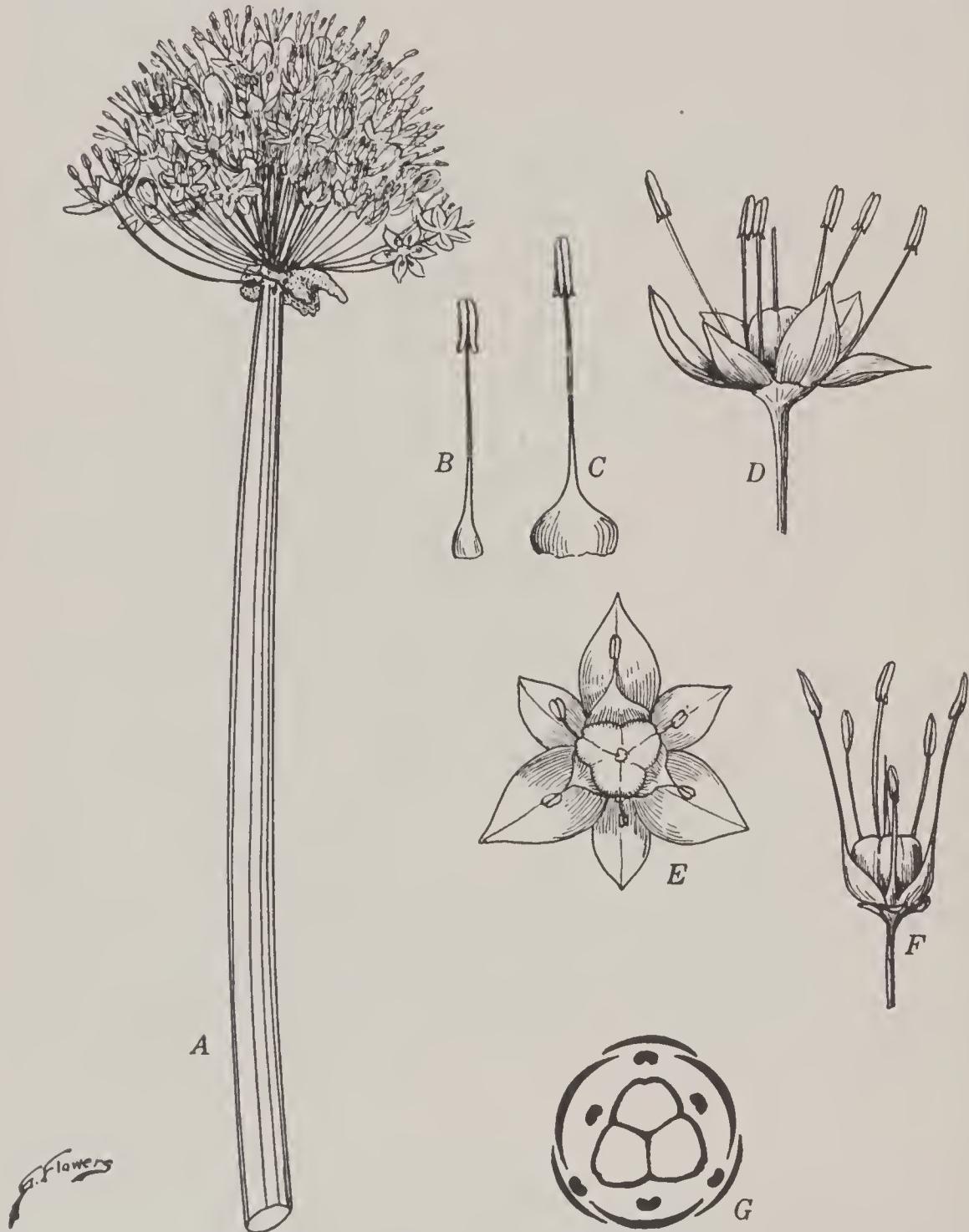


FIG. 82. A, the inflorescence; B and C, the inner and outer stamens; D, a single flower in side section; E, the same, face view; F, flower with perianth removed; G, floral diagram showing arrangement of parts.

are flattened tangentially, and roughly oblong in surface view. (Fig. 84, A, B.) The layer of perisperm that underlies the parenchymatous layer is hyaline, and the seed is filled with a horny

endosperm in which the coiled embryo lies embedded. (Fig. 83, A.) The endosperm cells are thick-walled, with a limited number of interconnecting pits. Sachs has shown that the thickening on the walls of the endosperm decreases during germination; and Cooley (3) has confirmed this, pointing out that the reserve hemi-cellulose, laid down on the wall as a secondary product, yields mannose on hydrolysis. The endosperm cells, which retain their protoplasmic contents, contain oil globules and protein, the latter being the first food to be withdrawn during germination. These cells, together with the cells of the haustorial portion of the coty-

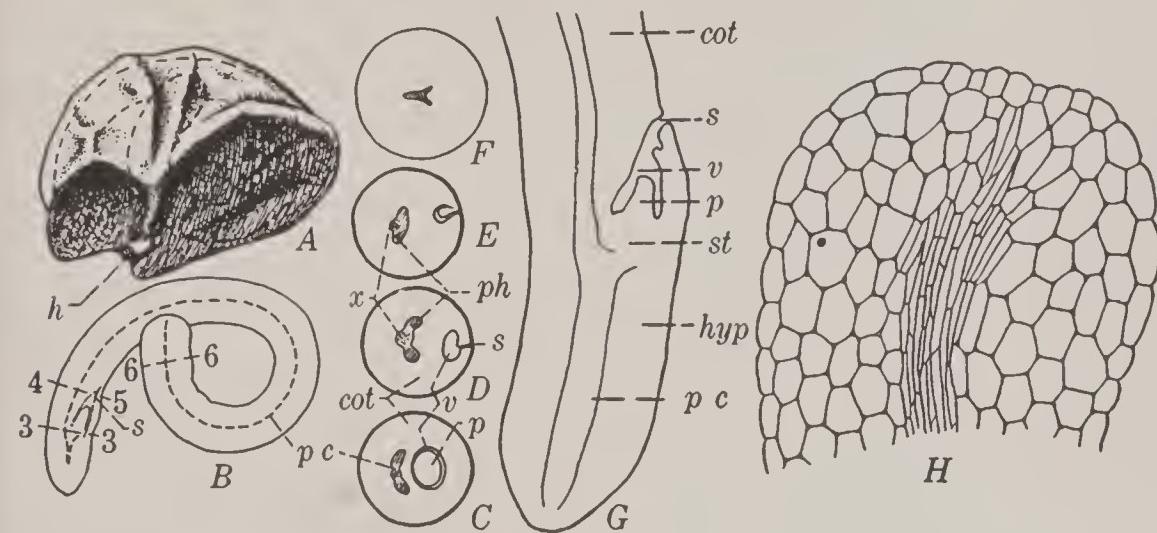


FIG. 83. A, the seed, dotted lines indicate position of the embryo; B, diagram of embryo; C, diagram of transection of embryo at level 3-3, in B; D, the same, at level 4-5, showing the slit; E, the same, showing variation in the slit; F, the same, at level 6-6; G, diagram of longisection of the lower portion of embryo; H, longisection through haustorial tip of cotyledon showing procambial cells extending to the epidermis which is without a cuticle: *cot*, cotyledon; *h*, hilum; *hyp*, hypocotyl; *p*, leaf primordium; *pc*, procambial strand; *ph*, phloem; *s*, slit in cotyledon; *st*, stem; *v*, cavity in hollow base of cotyledon; *x*, xylem. (After Hoffman.)

ledon, function in the absorption and transfer of food; and the endosperm cells do not collapse until all of the reserve cellulose is exhausted. (Fig. 83, H.)

THE EMBRYO. — The mature embryo is a curved cylinder about 6 mm. long and 0.4 mm. in diameter, the latter being uniform throughout except that the hypocotyl is pointed and the haustorial tip of the cotyledon somewhat rounded. (Fig. 83, B.) The curvature of the axis varies from crescentic to more than a complete circle, and, according to Hoffman, a 270° arc is the average. The hypocotyl is small and short, and the major portion of the embryo consists of the cotyledon which arises from the cotyledonary node

of the short stem axis. The epicotyl is surrounded by the basal sheath of the cotyledon and may bear a single, slightly developed leaf primordium prior to germination. (Fig. 83, G.) Near the base of the cotyledon there is a lateral slit leading into the cavity which, according to Sachs (15), occurs with equal frequency on the convex and the concave sides of the embryo. In his description of

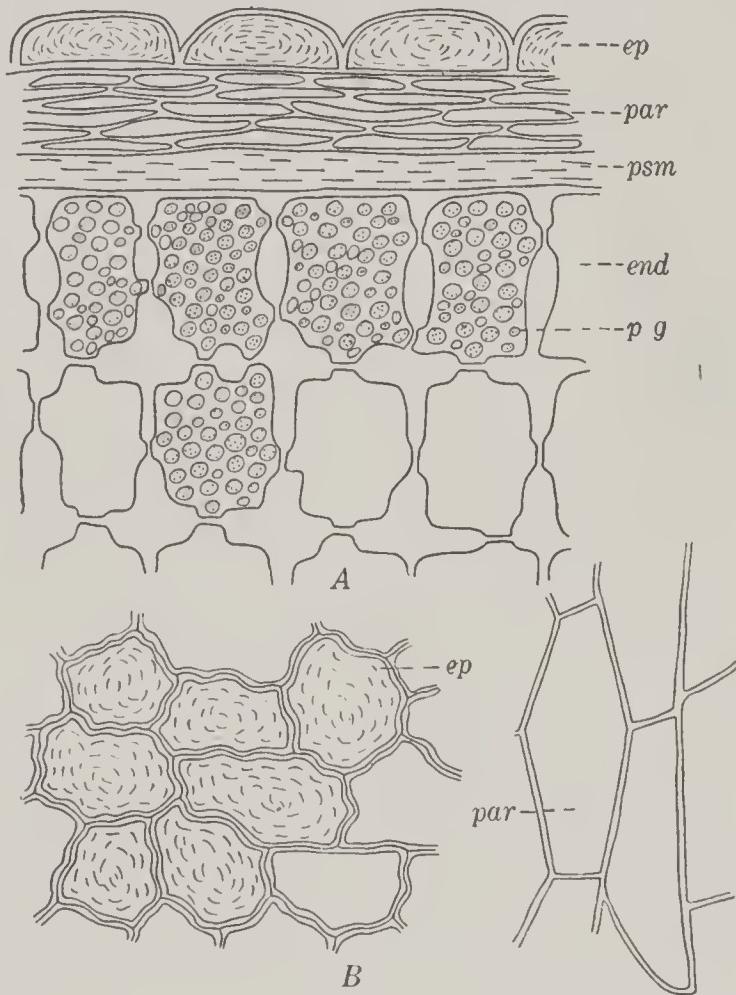


FIG. 84. *A*, transection of a portion of seed showing principal regions; *B*, surface view of the epidermis and parenchymatous region: *end*, endosperm; *ep*, epidermis; *par*, parenchyma; *p g*, protein granules; *psm*, perisperm. (Redrawn and rearranged after Kondo, Ohara Institute.)

the embryo, as seen in longisection, he recognizes five regions: (1) The peripheral or epidermal layer of thin-walled, parenchymatous cells. These are arranged in longitudinal rows covering the root and cotyledon; and, in the latter, stomata with guard cells may be found. (2) The parenchyma of the hypocotyl and cotyledons. (3) The single provascular strand which can be recognized by the long narrow cells that are filled with an albuminous material. (4) The meristematic regions occurring at the root tip and at the growing point of the epicotyl; and (5) the well-defined root cap.

DEVELOPMENT OF THE SEEDLING.—In germination, there is an initial elongation and growth of the lower and middle parts of the cotyledon resulting in the emergence of the root tip through the seed coat at the micropyle. (Fig. 85.) Within 24 hours, the hypocotyl has grown out through the seed coat; and the cotyledon

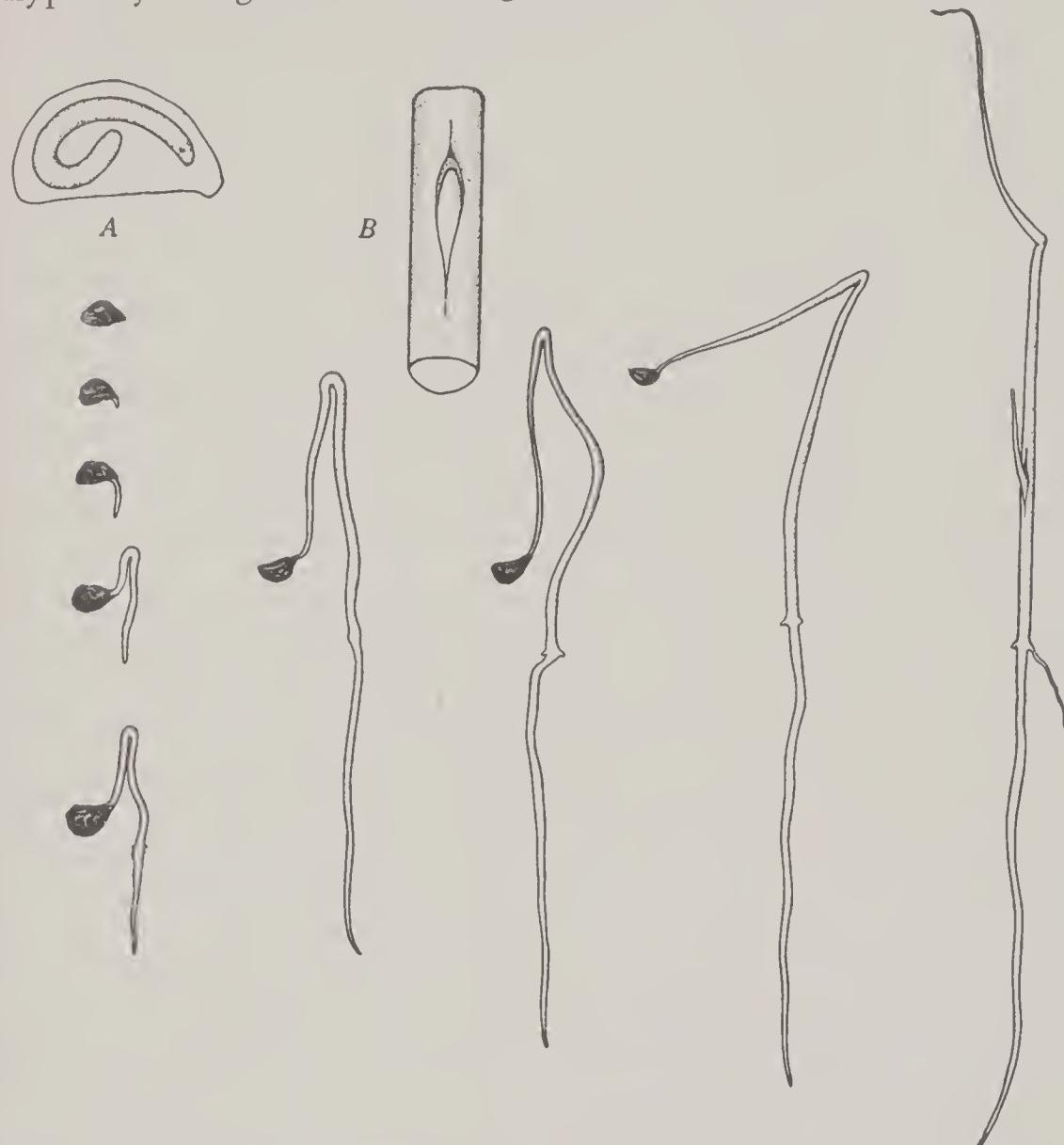


FIG. 85. The development of seedling: A, diagram of seed showing position of embryo; B, the emergence of first foliage leaf through the cotyledonary slit.

soon emerges except for its tip, which remains embedded in the endosperm and acts as a haustorium for the absorption of food. The emerging root tip is usually directed upward at first, owing to the shape of the seed; but after it has attained a length of from 3 to 5 mm., downward curvature takes place in the elongating parts of the seedling which already lie outside the seed. This results in the formation of a sharp bend in the cotyledon, which

is known as the "knee." One limb extends downward to the cotyledonary plate and the other to the terminal portion of the cotyledon which remains embedded in the endosperm.

Continued elongation of the two limbs brings the sharp "knee" above the soil surface; and then the growth of the two limbs becomes unequal, the one that joins the cotyledonary plate growing more rapidly than the one leading to the haustorial tip of the cotyledon. As a result of this unequal growth, the cotyledon assumes the shape of a bow in which the descending limb is curved and the ascending one is stretched like a bow string. The effect of this tension is to draw the tip of the cotyledon out of the seed and above the soil, so that it straightens, except for a slight kink which remains at the original locus of the knee. In some cases, when the soil is not too firmly packed, the seed may be lifted above the soil by the tip of the cotyledon. By this time, the cotyledon is green and photosynthetic. (Fig. 85.) The cotyledon attains a length of about 12 mm.; and, at the end of a week, the primary root may have grown downward from 2.5 to 5 cm. By the time seedling development is complete, the root may reach a depth of about 10 cm.; but it does not branch, and all later roots are developed adventitiously from the stem.

Root hairs are produced in abundance; and, just above the piliferous region at the top of the hypocotyl, the first two or three adventitious roots emerge through the cortex. According to Hoffman (7), they originate from the meristematic parenchyma of the inner cortical region. The first of these roots arises in this cortical sector just below the cotyledonary slit, the mode of emergence appearing to be both lysigenous and schizogenous. The second one usually originates at about a 90° angle to the right or left of the first; and if a third one develops, it is in a position diametrically opposite to the second. Subsequent adventitious roots originate like the earlier ones, but there is no regularity with respect to the order or place of their appearance.

While the root and cotyledonary development is taking place, the epicotyl is growing and the first foliage leaves elongate rapidly, keeping pace with the enlargement of the basal sheath of the cotyledon which surrounds them. Finally, the first foliage leaf pushes its way through the small longitudinal slit in the cotyledon. (Fig. 85, B.) By this time, the primordium of the second leaf has developed, and emerges through a slit on the outer side of the

sheath of the first foliage leaf which surrounds it. In this manner, the successive leaves are produced and emerge in rapid sequence. The stem axis from which the leaves arise elongates very slightly, and this slow growth, together with the development of the basal

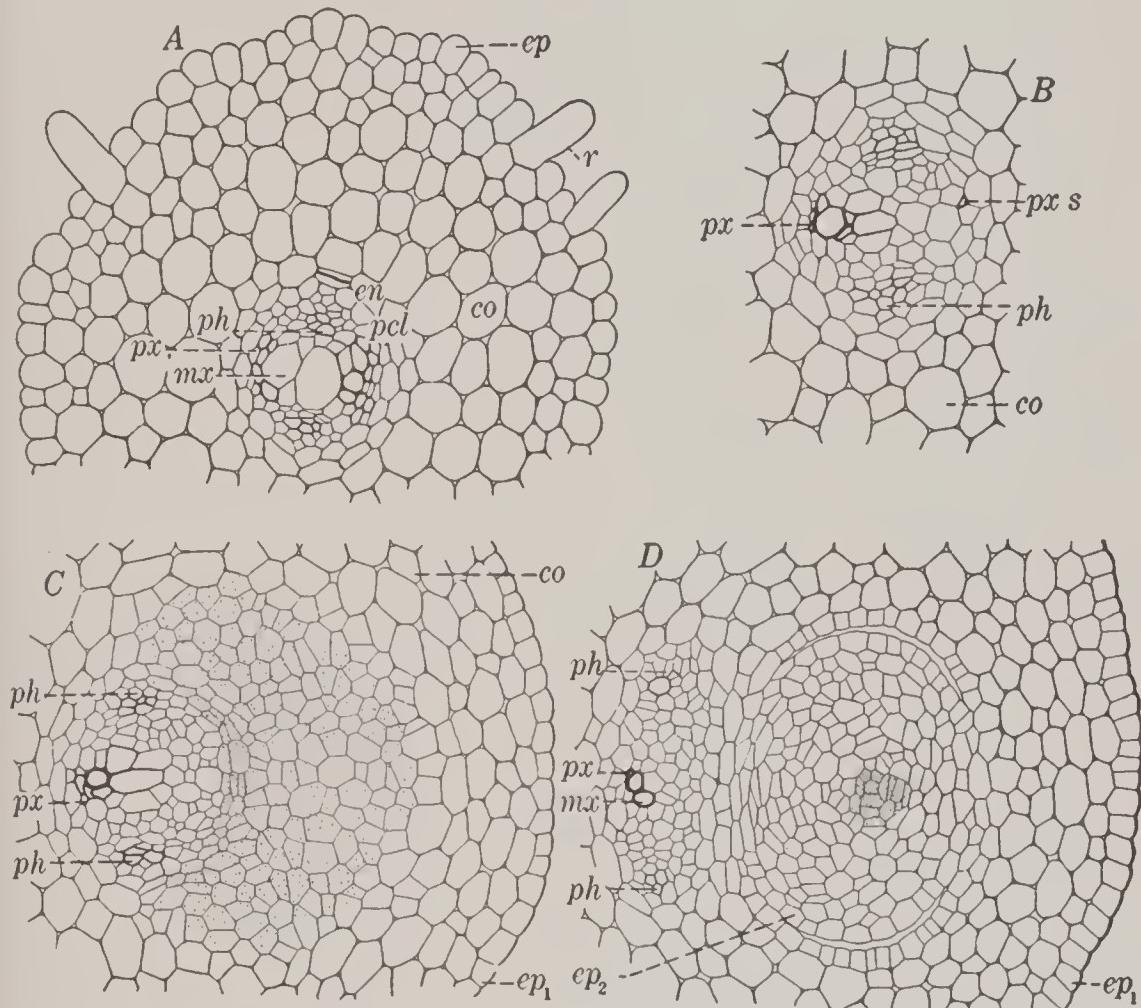


FIG. 86. *A*, transection through upper portion of primary root of six-day seedling; *B*, same, at higher level than in *A*, showing protoxylem, *px s*, consisting of a single cell; *C*, same, slightly above *B*, showing actively dividing cells of cortex (stippled) initiating first adventitious roots; *D*, same, at higher level than *C*, showing second leaf with first procambial strand (stippled) surrounded by cotyledon: *co*, cortex; *en*, endodermis; *ep*, epidermis; *ep₁*, epidermis of cotyledon; *ep₂*, epidermis of second leaf; *mx*, metaxylem; *pcl*, pericycle; *ph*, phloem; *px*, protoxylem; *r*, root hair. (After Hoffman.)

portions of the foliage leaves as storage regions, leads to the formation of the bulb.

THE PRIMARY ROOT. — The primary root has an exarch, radial protostele which is usually diarch, rarely triarch. At the level of the root hair zone, there are two protoxylem points which alternate with the two phloem groups and differentiate centripetally. (Fig. 86, *A*.) The central portion of the stele is at first parenchymatous; but, later in ontogeny, metaxylem elements are differen-

tiated consisting of one to five, usually two, large scalariform vessels; and when maturation of the stele is complete, there are no fundamental parenchyma cells remaining except the single-layered pericycle. Caspary strips are laid down early on the radial and end walls of the endodermal cells and are well developed in seedlings a week old. The cortical parenchyma consists of six or seven layers of thin-walled cells with intercellular spaces at their angles, and the epidermis is a single layer of cells, many of which elongate radially to form hairs.

The development of the root is similar to "type 2" as described by Janczewski (8) and modified by Treub (21). In this type, the meristem consists of two histogens, a well-defined plerome which gives rise to the stele, and, overlying it, a group of common initial cells two layers in thickness from which originate the cells of the root cap, epidermis and cortex. The plerome consists of a layer of a few cells from which the pericycle is first differentiated. Then as the protoxylem is differentiating, the cells of a centrally located axial row enlarge, especially in the longitudinal direction, without further division; while the adjacent cells continue to divide. These large cells finally mature as segments of a metaxylem vessel or vessels. (Fig. 87, C, D.)

One or two periclinal divisions of the undifferentiated cells enlarge the stele so that it is from five to ten, most commonly seven, cells in diameter. The pericyclic cells may be somewhat shorter than the adjacent endodermal and cortical cells, and can be distinguished from the provascular cells which lie immediately centrad to them by the small caliber of the latter.

Distal to the plerome is a meristematic region three to six cells in diameter and two to four cells in depth. The cells of the inner layer or layers of this region function as a periblem and produce the cortex, which reaches its mature width as a result of one or more periclinal divisions. The cells in this region divide in the transverse plane more frequently than do those of the stele; and less so than the epidermal cells, so that they are intermediate in length. The lateral cells of this same meristematic region produce a single layer of epidermal cells which divide only anticlinally. The outermost layer of the meristematic region cuts off the cells of the root cap. This consists of several dome-shaped layers of cells overlying one another, the outermost being the oldest and largest. At the apex of each layer, the cells are larger, slightly more numerous, and

axially elongated so that the cap is wedge-shaped in outline. In the central portion of the root cap, where there is the least variation

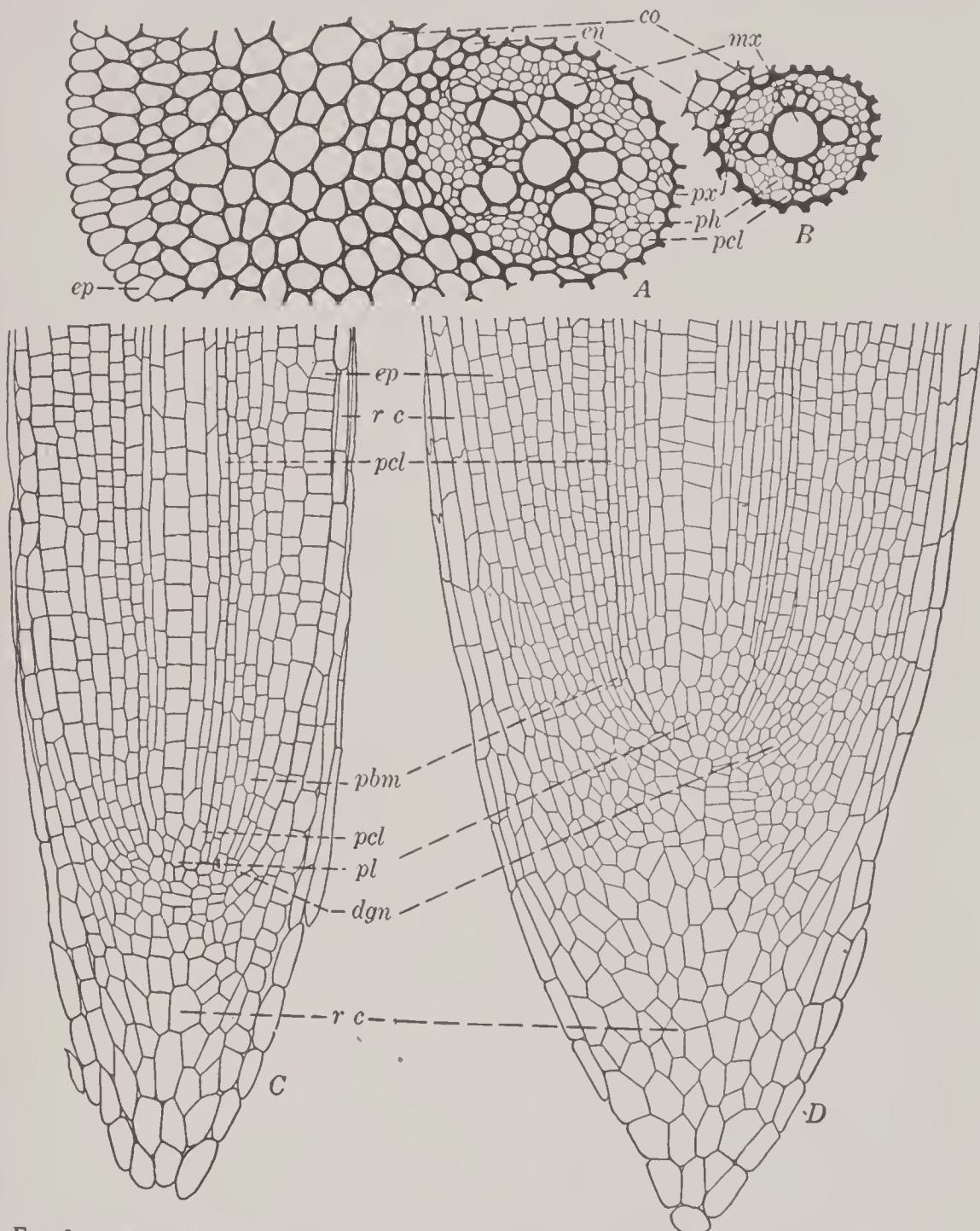


FIG. 87. *A* and *B*, transections of mature portions of adventitious roots showing pentarch and tetrarch types; *C*, longisection of primary root grown in soil; *D*, adventitious root grown in water: *co*, cortex; *dgn*, dermatogen; *en*, endodermis; *ep*, epidermis; *mx*, metaxy-cap; *pbm*, periblem; *pcl*, pericycle; *ph*, phloem; *pl*, plerome; *px*, protoxylem; *rc*, root

in the size of the cells, a longisection shows two to four irregularly vertical rows of cells, each of which may be traced back to a single cell of the histogen. (Fig. 87, *D.*)

THE STRUCTURE OF THE COTYLEDON. — In the growth and development of the cotyledon, Hoffman observed that there is "apparently no localized meristematic region in any part of the cotyledon, cell divisions occurring throughout its entire length, although the cells at each end reach their full size later than the others." As this general growth takes place, the cells become vacuolate, enlarging to six or eight times their embryonic length; and, subsequently, they may divide two or three times. He found no mitotic figures during the first five days of development, and concluded that growth up to this point is mainly the result of cell enlargement. A few days later, mitoses occur in large numbers in all tissues, the last region to initiate nuclear and cell division being that part of the cotyledon adjacent to the seed. At the end of two weeks, mitotic figures are again lacking.

The cotyledon above the lateral opening has a single, centrally located vascular strand extending to its extreme tip. This is surrounded by several rows of cortical parenchyma which are in turn bounded by the epidermis. The tip of the cotyledon is haustorial in function, and the epidermis at this point is without a cuticle. (Fig. 83, *H.*)

The vascular anatomy of the cotyledon and its relation to that of the root has been described by Chauveaud (2) and Hoffman (7), the account of the latter differing from the former chiefly with respect to the ultimate disposition of the protoxylem elements. The stelar organization of the hypocotyl, up to the cotyledonary plate, resembles that of the primary root, and the two protoxylem points of the primary xylem strand are alternate with the two primary phloem groups. In the center of the stele are a few large parenchymatous cells which later mature to form the two or more large metaxylem vessels. (Fig. 86, *A.*)

The differentiation of the xylem of the cotyledonary bundle begins at a level slightly above the slit and proceeds from this point upward and downward at about equal rates. As first noted by Sachs (15), the xylem of the cotyledonary bundle is continuous with one of the exarch xylem strands of the hypocotyl, and the phloem of this bundle is joined with both of the phloem groups of the hypocotyl. The differentiation of the other primary xylem strand of the stele is retarded at the point where the vascular system of the first foliage leaf later differentiates and anastomoses with it. At the base of the cotyledon, the vascular portion of the axis is

slightly enlarged, the metaxylem vessels are somewhat smaller, and the alternate, radial position of the xylem and phloem still persists. (Figs. 83, C; 86, B.)

The development of the cotyledonary xylem is exarch throughout. In most cases, the protoxylem consists of spiral elements, although some annular elements may occur; and annular thickenings are frequently present in the tapering ends of the tracheids. The cotyledonary bundle has one protoxylem point, and a band of metaxylem is later differentiated on each side of the youngest or most recently formed protoxylem. This results in the formation of a Y-shaped xylem region with an accompanying zone of primary phloem at the end of each arm of the Y. The orientation of the xylem and phloem is shown diagrammatically at successively higher levels in the cotyledon in Figure 83, C-F. In some cases, the xylem is separated into three or four groups by parenchymatous cells; while, in others, the Y-shaped configuration may be flattened so that it appears like a short-stemmed T.

The maturation of the phloem occurs first at points farthest removed from the protoxylem. Chauveaud (2), in describing the development of the cotyledonary bundle in seedlings eight to ten days old, reports a disintegration of the protoxylem as the metaxylem differentiates, attributing this to a complete resorption of the protoxylem elements and their replacement *in situ* by metaxylem. Studies of this region by Hoffman, especially in longisection, indicate that there is not a complete resorption of these elements; but that "the protoxylem vessels become so stretched that the walls between thickenings collapse; and, in transection, the vessels are seen as only a very small patch of cellulose, easily overlooked." This stretched protoxylem is more difficult to find as the cotyledon becomes older; but can be seen in longisections of material less than four weeks old, at which time the second and third leaves have appeared and the cotyledon has begun to wither from its tip downward toward its base.

ADVENTITIOUS ROOTS. — All the roots, except the primary one, are adventitious in origin. During the development of the seedling, the first of these arises from the meristematic region of the inner cortex. (Fig. 86, C.) Subsequent roots originate in a similar manner, being produced in great abundance so that a plant five months old may have up to a hundred root primordia and roots. The later-formed roots originate in the pericycle, rather than in the

inner cortical region. This is not a single layer, but consists of a meristematic region adjacent to the cortex. (Fig. 88.) The cortical parenchyma of the adventitious root is continuous with that of the crown stem, and, as the root elongates, it pushes

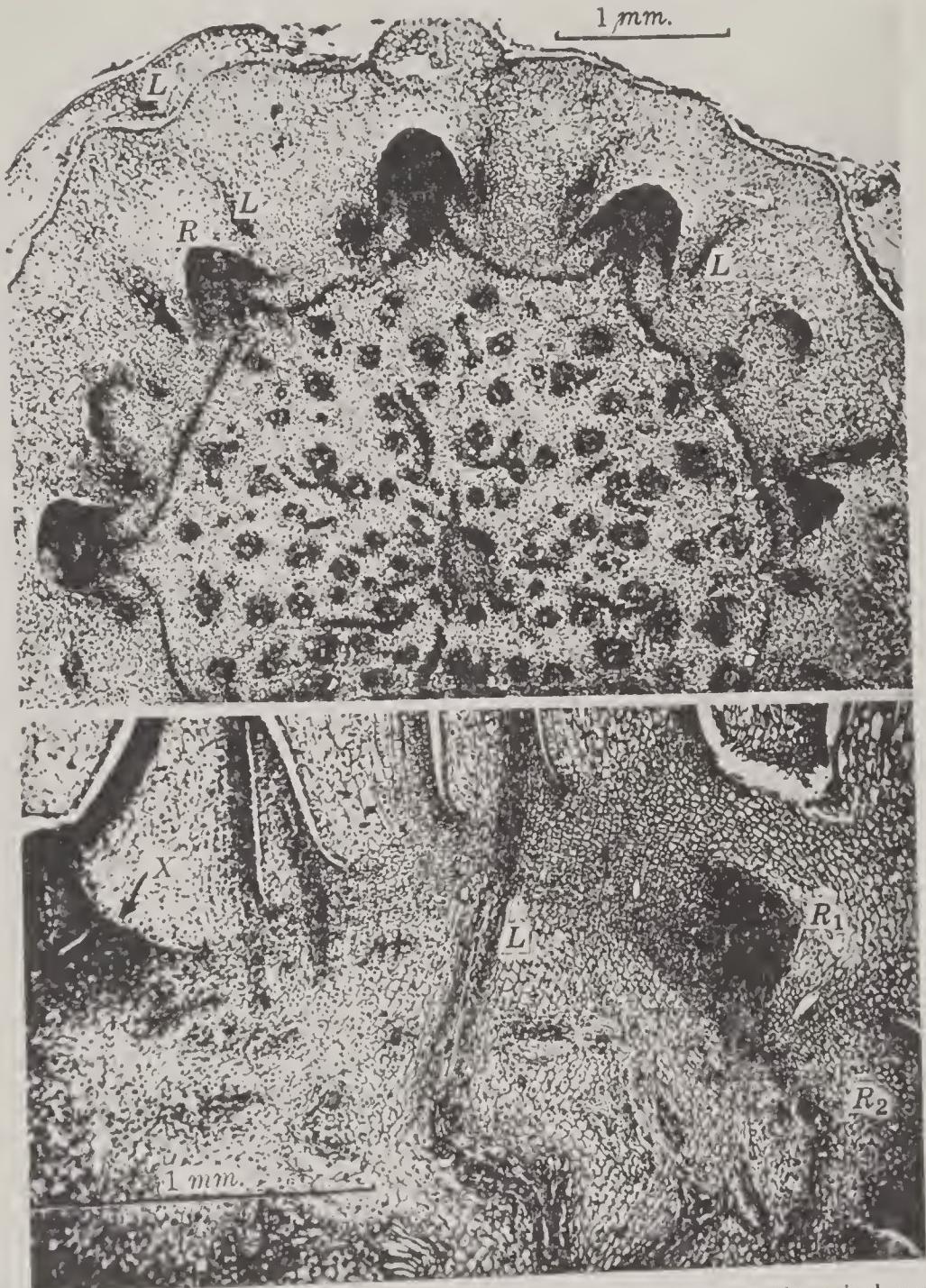


FIG. 88. Above, transection of stem five months old, slightly below the apical meristem, showing origin of four adventitious roots, R , which are continuous with the outer procambial tissue. The seven cycles of bundles in the stelar portion extend to leaf blades and sheaths, one cycle for each leaf. The vascular bundles of sheath, L , are shown in partial longisection in cortex.

Below, longisection through apical meristem showing adventitious roots, R_1 and R_2 , apical meristem, X , and vascular bundle of a sheath, L . (After Hoffman.)

through the outer cortical cells, finally penetrating the bases of two or three fleshy leaf sheaths. In some instances, the root penetrates the inner epidermis of a leaf sheath but fails to pierce the outer, and the root grows upward through the mesophyll, eventually dying when the sheath becomes desiccated. The emergent adventitious roots may branch after attaining a length of 10 to 15 cm.; but, during the first year, the older roots, as well as the lower part of the crown stem and outer leaves, shrivel and die so that the base of the bulb appears somewhat flattened.

The adventitious roots are tetrarch, pentarch, or hexarch, the pentarch being most common; and all three types may occur in the same plant. (Fig. 87, A, B.) Their development resembles that of the primary root, the chief difference being the larger histogenic region and the correspondingly greater number of cells formed.

THE VASCULAR ANATOMY OF THE CROWN STEM. — The structure of the entire hypocotyl is root-like; and, near its top, the two protoxylem strands separate, one continuing into the cotyledon, while the other ends blindly beneath the point of divergence of the primordium of the second leaf. (Fig. 86, B.) Above the point at which the hypocotyledonary xylem terminates, the xylem of the cotyledonary bundle and of the stem develops in one direction — away from the protoxylem of the cotyledon and toward the center of the stem axis. About ten days after germination, the very short stem contains no mature xylem, except that of the cotyledonary bundle; and approximately ten more days are required before the xylem of the trace of the second leaf is completely differentiated in the first internode. The elements of this trace are reticulate cells about three times as long as wide.

All the bundles of the stem are common, representing the downward divergence of leaf traces; and the vascular arrangement of the stele is determined largely by the manner in which the leaves are differentiated. As each leaf matures, the bundles in its cylindrical sheath extend into the stem and anastomose with the ring of vascular tissue. The bundles of each successively higher leaf trace are vertically connected with those below, so that the central pith is surrounded by a cylindrical stele consisting of a complex network of vascular strands. The larger bundles of each leaf trace are connected directly with the inner perimedullary portion of the vascular cylinder, while the smaller ones are anastomosed with the peripheral bundles of the stele.

In longisection, the stem appears somewhat heart-shaped, since the successively formed parts have increasing diameters and grow more rapidly than the terminal meristem. The thick, parenchymatous cortex is traversed by numerous traces of adventitious roots which form an almost continuous zone surrounding the stele; and the leaf traces are separated from them by a layer of parenchymatous cells so that there is no direct connection between the two vascular systems. The basal stem bundles are usually amphivasal, with a layer or two of parenchymatous cells separating the phloem from the surrounding xylem; but higher in the stem, the amount of xylem on the outer face of the vascular strand diminishes and the bundles are collateral.

ONTOGENY OF THE LEAF. — Each leaf develops as an upright, hollow cylinder, one side of which grows more rapidly than the other forming the blade. The leaf primordium arises as a dome-shaped mass of cells which grows more rapidly than the center of the axis and begins to partially enclose the growing point. (Fig. 90, *A-G.*) As its eccentric growth continues and one side becomes higher, the entire periphery of the growing region forms a fold which grows upward and around the axis to constitute the basal sheath of the young leaf. While this is taking place, another primordium arises within the first, and its blade grows at the same rate as the more slowly developing portion of the periphery of the enclosing leaf. (Fig. 90, *H, I.*) In this manner, the vertically oriented, cylindrical base of each young leaf completely surrounds younger leaves which in turn enclose the apical meristem.

As the differentiation of the sheath and blade proceeds, there is a rapid increase in the diameter of the growing region of the axis, and the base of the newly formed leaf is pushed farther away from the center of the stem. By the time the next younger leaf is differentiated, no more periclinal walls are formed, and further increases in the thickness of the sheath, which becomes the fleshy bulb scale, are due to cell growth and to the formation and enlargement of intercellular spaces.

The orifice of the sheath is surrounded by a thin membrane extending around its upper edge, including the side bearing the blade. It is an outgrowth of the blade, five or six cells in thickness, which is usually devoid of vascular tissue. In the first six or eight leaves, elongation is greater than in the later formed ones; and the openings become much stretched longitudinally so that their margins

are in contact with one another, closing the cavity within until the next younger leaf pushes through it. In the later leaves, the tip of the blade may be pushed through the orifice of the next older



FIG. 89. Median longisection, except at the bottom, through the plane of phyllotaxy of five-months old stem: *B*, transection through a perimedullary bundle; *C*, cortex; *L*, leaf trace; *P*, pith; *R*, root trace, *X-X*, sheath and blade of one leaf. (After Hoffman.)

leaf while both are themselves enclosed within the sheath of a still older one. (Fig. 89.)

Hoffman has found that in the growth of the first leaves, the blade attains a considerable length before the sheath begins to elongate appreciably. Growth takes place at about equal rates in all parts of the blade, but the leaf tip is the first part to cease

elongation, while the base of the sheath remains meristematic longer than any other part. Thus,

"in the earliest stage of development the entire leaf is meristematic; at a later date, only the sheath and base of the blade; and still later,

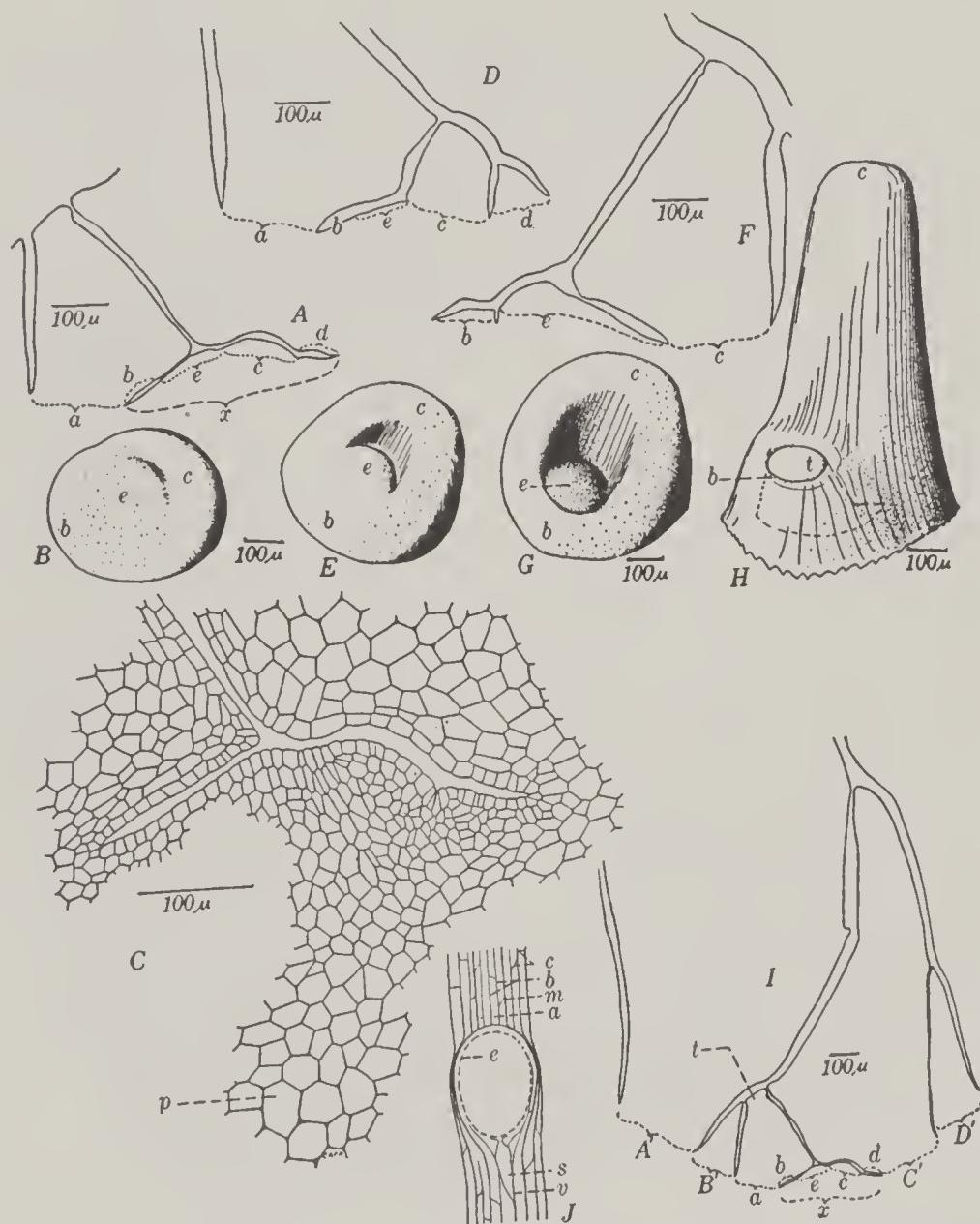


FIG. 90. *A*, longisction through growing point of axis shown in *B*; *a* and *d* are opposite sides of same leaf which overgrow central region, *b*, *c*; *B*, earliest stage in leaf differentiation; *C*, cell detail of region, *x* in *A* and *I* (plane of cell division marks boundary between regions *e* and *c*); *D* and *E*, one side, *c*, has outgrown *e*, and the other side, *b*, is beginning to overgrow it; *F* and *G*, both sides, *b* and *c*, overgrowing axis, *e*, which is beginning to elongate; *H* and *I*, more rapidly growing side, *c*, is forming blade of leaf while *b* forms the sheath or bulb scale; *J*, diagram of vascular system in mature leaf at orifice: *a*, adaxial side of blade; *b*, branches of larger bundles; *c*, cross-connections; *e*, edge of orifice; *m*, continuous bundle of sheath and blade; *p*, pith; *s*, outer side of sheath; *t*, tip of younger leaf; *v*, bundles ending blindly under orifice. (The small letters in *A-H* correspond to *A'*, *B'*, *C'*, *D'* in *I*; while *a* and *d* in *I* represent blade and sheath sides of a younger leaf. (After Hoffman.)

only the base of the sheath. The lowest portion of a half-grown blade remains meristematic until the leaf is nearly grown, however, so that this region gives rise to a large share of the blade. Any one leaf, after it reaches a length of three centimeters, attains its mature length in a few days."

In the development of the leaf, mitoses, indicating continued cell divisions, may occur in all parts, even after intercellular spaces are formed. Transverse divisions and growth of the surrounding parenchymatous cells cause the intercellular spaces to become enlarged and much elongated throughout the entire leaf. There is a peripheral zone in which the cells enlarge radially rather than longitudinally; and, in the mature leaf, these form two or three subepidermal layers of columnar cells which are comparable to the palisade region found in dicotyledonous leaves. (Fig. 91, B.)

The parenchymatous cells central to the chlorenchyma do not keep pace with the growth of the latter, and a large central cavity develops which extends through the entire length of the blade. (Fig. 91, A.) Prior to the formation of the cavity, the inner cells are alive, although the volume of the intercellular spaces formed between them is probably greater than the volume occupied by the cells themselves. Newcombe (12) has described cavity formation in onion and other plants, and regards the initial stages which occur during the primary growth of the leaf as being schizogenous. The final ones are lysigenous, and result from the death and collapse of the centrally located parenchyma cells which by their disintegration add to the size of the central cavity.

THE MATURE LEAF. — The blade of the mature leaf consists of the epidermis, the palisade layers, the vascular bundles, and eight or ten rows of spongy parenchyma which surround the central cavity. (Fig. 91, B.) The development of the xylem in the procambial strand is endarch, and differentiation proceeds rapidly from the base of the leaf to its tip so that the first protoxylem elements are mature throughout the entire length of the leaf before any of the metaxylem is completely developed. Nearly all of the primary xylem elements have spiral thickenings.

The cotyledon has a single vascular bundle, and the number increases in successive leaves, the second leaf having five bundles, the third usually eight. Each of the older leaves has two more bundles than the preceding one until, in the sheath of a mature bulb scale, there may be 40 or more. The bundles are arranged

around the periphery of the leaf blade or base and are parallel throughout its entire length. There are many small branches and cross-connections between adjacent bundles which arise in the rows of parenchymatous cells that surround and separate the bundles.

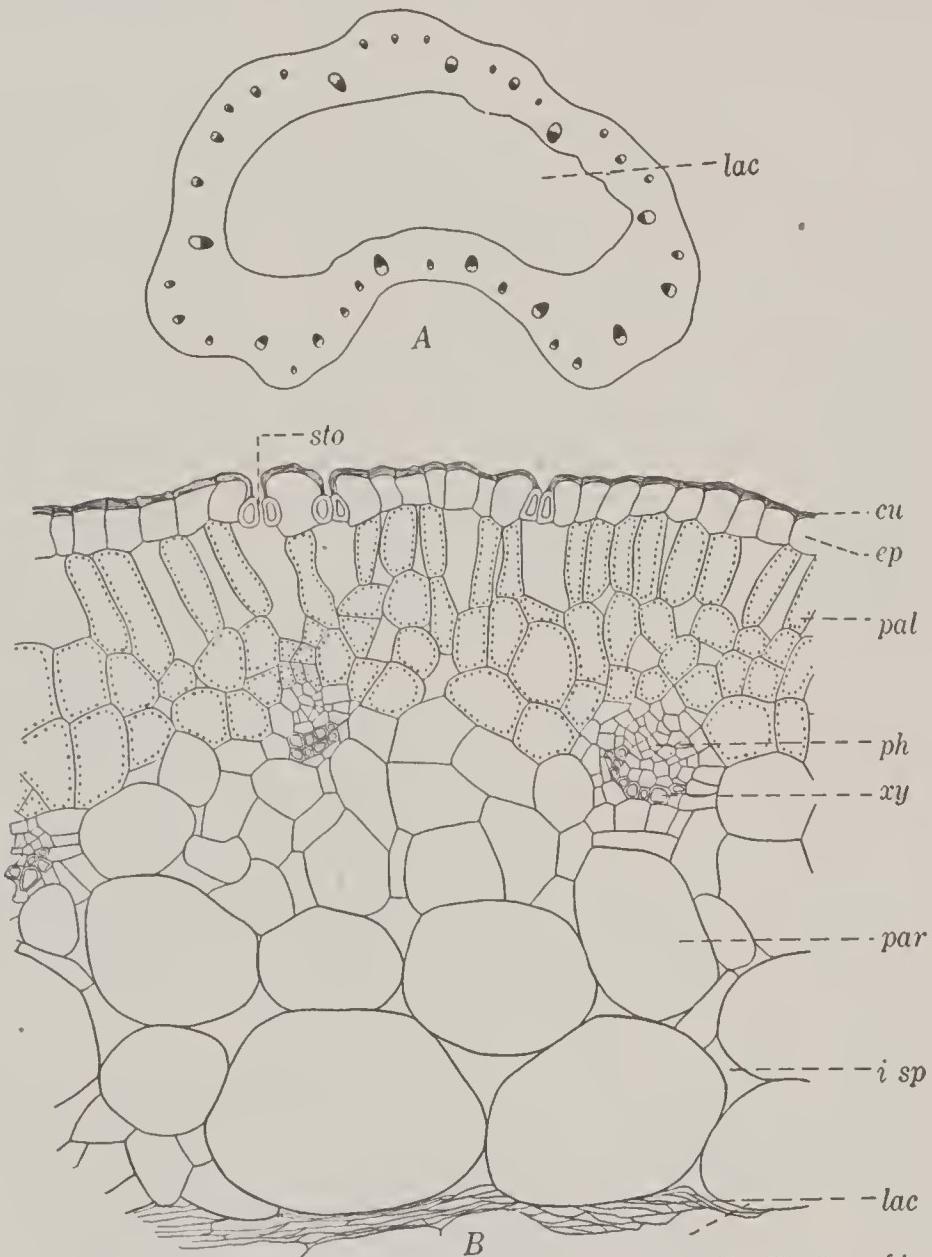


FIG. 91. A, diagrammatic transection of the lamina showing distribution of bundles and large central lacuna; B, a section of A showing cellular detail: cu, cuticle; ep, epidermis; i sp, intercellular space; lac, lacuna (broken down parenchymatous cells are shown on the margin of lacuna in B); pal, palisade cells; par, parenchyma; ph, phloem; sto, stoma; xy, xylem.

There are relatively few transverse veinlets in the lower half of the outer sheaths of the mature bulb, but many occur in the upper parts. The unthickened sheaths of a young onion have numerous cross-connections at all levels. Both large and small bundles may originate blindly and then anastomose with larger ones, while some of the

smaller ones may end at the base of the blade without joining other veins. In the outer sheaths, the bundles frequently appear green because of a layer of chlorenchyma which partially surrounds them.

In the mature leaf, the orifice leading to its basal cavity is oval in outline, and appears to be laterally placed owing to the greater elongation of the sheath on the side bearing the blade. At the base of the sheath, the distribution of the vascular bundles is fairly uniform; but near its top, they become more closely aggregated on the side of the sheath from which the blade extends. On the opposite side, there are one or two smaller bundles which, after branching several times and producing cross-connections, end blindly under or around the margin of the sheath. On each side of these smaller bundles is a larger one which parallels them up to the orifice and then curves around its edge. (Fig. 90, J.)

LACTIFEROUS CELLS. — The cotyledon and all other leaves develop longitudinal rows of lactiferous cells. They first appear early in the ontogeny of the plant, and may be found in a longisection of the cotyledon about 14 days after germination. In the leaf base, they are almost invariably separated from the epidermis by two layers of parenchyma, rarely by only one; but in the green tubular portion of the blade, they may be more deeply located, lying just within the chlorophyllose palisade tissue. (Fig. 92, D.) Hanstein (5) described these structures in various species of *Allium* and called them "vesicular-vessels." Later, Rendle (14) pointed out that the term "vessel" is not appropriate in this case, since the latex-containing cells are "not cell-fusions, and continuity between the contents of adjacent members can very rarely be seen." He suggested the term "laticiferous cells" for these structures, which has been shortened to "lactiferous cells" by Hoffman.

Each row of lactiferous cells is parallel to the epidermis; and in their early stages of development, the transverse septa are not pitted; but become so as the leaf enlarges and the cells elongate. (Fig. 92, A, D, E.) In the succulent portion of the leaf, these cells do not elongate much, and they are extremely short at the base, where the longitudinal series may be irregularly connected by cross unions. (Fig. 92, F.) Both Hanstein (5) and Rendle (14) state that rows of lactiferous cells may occur side by side; and in such cases, the longitudinal wall separating them is also pitted; but where parenchyma abuts these cells, the dividing walls are unpitted. (Fig. 92, B.)

The lactiferous cells end near the extreme base and apex of the leaf respectively, and there is no evidence of any connection between

them and the vascular bundles or the assimilating tissue, nor do they follow the general course of the former. The contents of the cells is a more or less granular turbid fluid which appears on a cut surface of the leaf bases as a pale milky liquid, but is clearer and more watery in the green leaves. The latex does not contain any food substances, according to Rendle, but seems to consist of a compound that is easily hydrolyzed to allyl sulphide. Apparently it is an excretion product, and the function of these cells is excretory or protective.

Owing to the superficial resemblance between the lactiferous cells and sieve tubes, it has been suggested that they may function in conduction; but they appear to be nothing more than rows of excretory sacs that are sealed up by the deposition of callus very early in ontogeny. Rendle has observed that "even before the transverse septa become conspicuously pitted, callus-formation occurs upon them; at first usually as

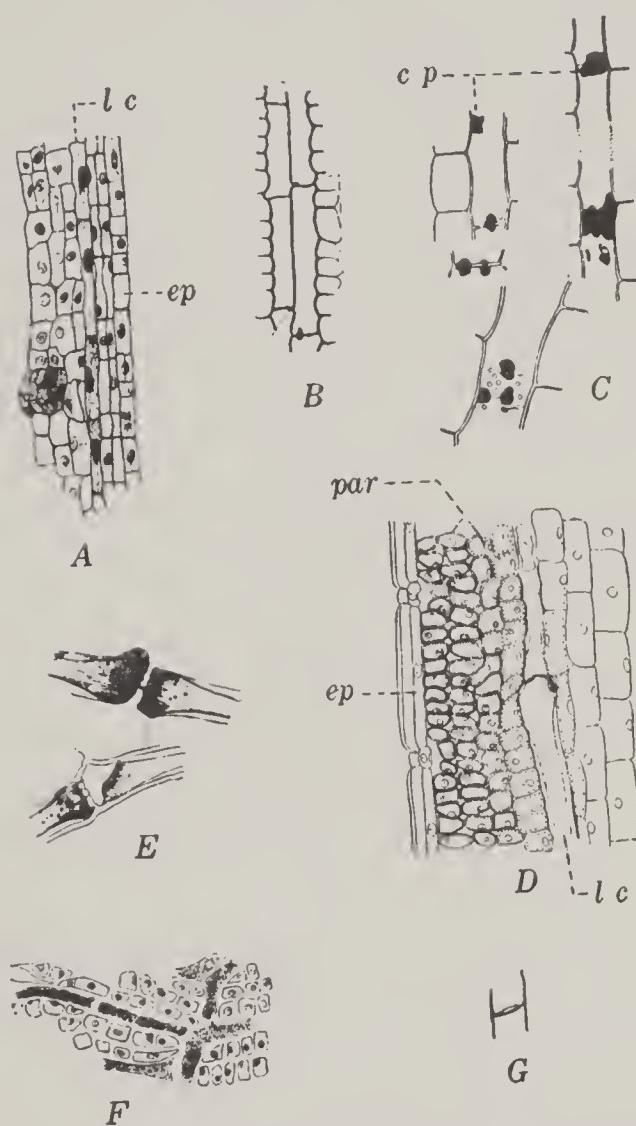


FIG. 92. The development of lactiferous cells in *Allium*. *A*, longisection of base of young inner leaf; *B*, tangential section of an inner succulent leaf prior to elongation; *C*, tangential sections of base of an outer leaf showing callus formation on transverse septa and occasionally on side walls of cells; *D*, longisection of a portion of green blade showing location of lactiferous cells; *E*, tangential sections of base of an outer succulent leaf showing the pitting in swollen transverse septa; *F*, tangential section of unelongated leaf showing cross unions between two rows of lactiferous cells; *G*, transverse septum from young leaf of the shoot enclosed in a germinating onion: *c.p.*, callus plug; *ep.*, epidermis; *l.c.*, lactiferous cell; *par.*, chlorophyll parenchyma. (After Rendle, *Ann. Bot.*)

small plugs, afterwards often of a more irregular form and sometimes spreading more or less over the whole plate." (Fig. 92, *B*, *C*.)

STOMATA. — Stomata are numerous in the epidermis of the cotyledon less than a week after germination. In the development of the stoma, a mother cell is cut off from one end of an epidermal cell so that it is approximately square in surface view. This cell by one longitudinal division forms the guard cells which subtend the stoma. In the mature leaf, the guard cells are sunken beneath the surface of the adjacent epidermal cells which partially overgrow them and develop a thick, lamellated cuticle which may exceed half the radial dimension of the cells.

THE BULB. — The bulb consists of a short stem which bears a series of thickened leaves and leaf bases, together with the cycles of adventitious roots which have been described as arising from the cortical and pericyclic regions. (Fig. 93.) The arrangement of the leaves is concentric so that the older ones surround the younger, and the apical meristem is located at the center of the bulb. The blades of the leaves comprising the bulb may be photosynthetic or they may dry down entirely. In a full-sized mature bulb, some of the inner leaves do not develop an elongated blade, and the functional blades of the outermost six or seven leaves become dry and break off so that only the sheaths remain. These protect the fleshy storage leaves which surround three or four leaves with short undeveloped blades; and centrad to the latter are successively younger leaves with longer blades.

In the spring, the youngest leaves continue development. The storage leaves outside them also elongate, especially at the base, but their green blades remain relatively small. As the inner leaves are growing, the outer storage leaves dry progressively from the top of the sheath to its base because of the withdrawal of food reserves and moisture. Preceding and accompanying this development, numerous adventitious roots arise from the periphery of the stem and penetrate the soil. These remain functional throughout the life of the plant.

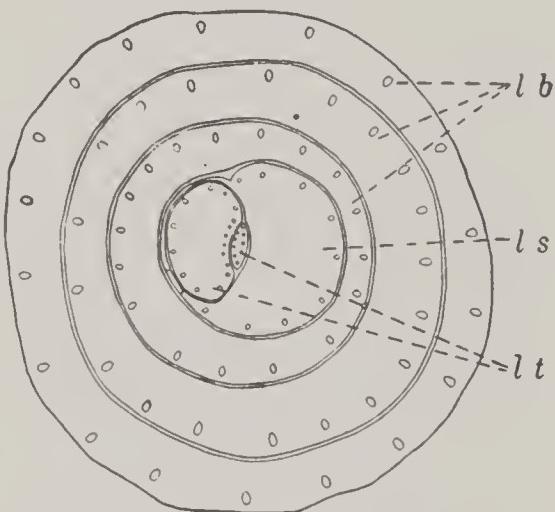


FIG. 93. Diagrammatic transection of young bulb showing relation of leaves to each other: *lb*, leaf bases; *ls*, leaf sheath; *lt*, leaf tips.

THE FLORAL AXIS.—The flowers are borne in simple umbels at the apex of a floral stem which is commonly hollow when mature, and somewhat swollen at its middle or near the base. (Fig. 94.) The number of floral stems per plant may vary from



FIG. 94. Field of Yellow Globe onions. (Courtesy of Ferry-Morse Seed Co.)

one to twenty or more, depending upon the variety and the size of the mother bulb. In the development of the floral axis, the first structure to arise is the bract which encloses it. The primordium of this bract originates at a point opposite the youngest leaf blade, and it is not until the central axis begins to elongate to form the flower stalk that it can be determined whether the leaf-like structure is a bract or another vegetative leaf. The bract encloses the

meristematic growing point from which the flowers arise; so that, during early ontogeny, the flower cluster is protected by the involucre as well as by a series of bracts which lie within. Each bract surrounds the primordia of several individual flowers.

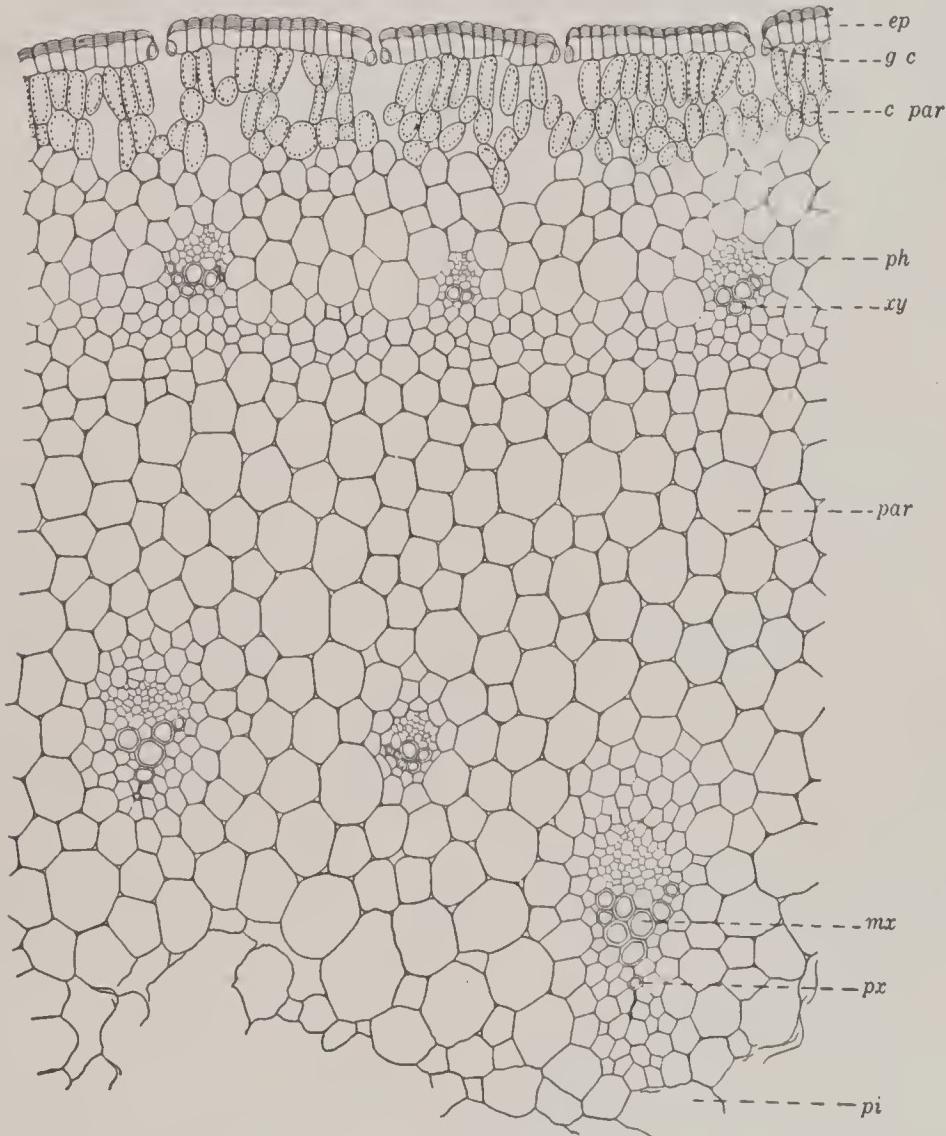


FIG. 95. A sector of a transection of flower stalk near base: *c par*, chlorophyll parenchyma; *ep*, epidermis; *g c*, guard cell; *mx*, metaxylem; *par*, parenchyma; *ph*, phloem; *pi*, pith; *px*, protoxylem; *xy*, xylem.

In the mature flower stalk, the epidermis is protected by a thick lamellated cuticle; and the cells are radially elongated with thin radial walls and somewhat thickened inner tangential ones. The sunken stomata are numerous and open into substomatal cavities in the palisade tissue. (Fig. 95.) The chlorophyllose region consists of one or more rows of palisade cells and a row or two of underlying spongy parenchyma in which lactiferous cells, such as are found in the leaf, are located. The parenchymatous cells centred to the chlorenchyma are large and surround the outer cycle

of vascular bundles. This region is bounded centripetally by a band of small, compact, parenchymatous cells which form a complete ring. Within this zone are the large, loosely organized cells which surround the inner cycle of vascular bundles. At maturity, the central region breaks down schizogenously, and a large lacuna is formed similar to that in the blade of the leaf. The collateral bundles consist of primary sieve tubes and companion cells, and primary xylem elements that are annular, spiral, and reticulate.

ONTOGENY OF THE FLOWER. — Jones and Boswell (9) have investigated the formation of flower primordia and the relation of the time of planting onion sets or young bulbs to their differentiation. Examination of the bulbs for the development of flower primordia indicates that in general the flower primordia are differentiated early in the spring under conditions prevailing in College Park, Maryland. This occurs regardless of "whether or not the bulbs are planted in the fall or early in the following spring, having been kept in storage over winter." It was also observed that "fall planted bulbs, which made a luxuriant foliage development before the differentiation of flower primordia, produced uniformly taller and heavier seed-stalks with a heavier set of blossoms, than was obtained from the spring planted bulbs." Under California conditions, bulbs planted in December differentiate the floral axes in February.

Jones and Emsweller (10) have worked out the floral development, and the following account is based in part upon their investigations. After the differentiation of the involucral bract, numerous membranous bracts arise on the meristematic surface of the tip of the floral axis, and these enclose the clusters of flower primordia in their early stages. (Fig. 96, *H*, *I*.) Each of these areas is somewhat elevated and kidney-shaped, and it is from them that the individual flowers arise.

The flower primordium develops as a slight projection on the meristematic surface, which becomes globose and later elongates slightly so that it is circular in transection and convex at its apex. (Fig. 97, *B*.) As growth proceeds, the primordium becomes triangular in transection as a result of the differentiation of the outer perianth segments and the outer stamen whorl which is the first to be formed. (Fig. 97, *C*.) At each angle of the triangular primordium, there is differentiated a perianth segment; and in the axil of each is a primordium of one of the stamens of the outer

whorl. (Fig. 97, E, G.) There is sometimes a lag in the development of the primordia of the outer stamens; so that the first lobe of the perianth may be well developed before the primordium of the

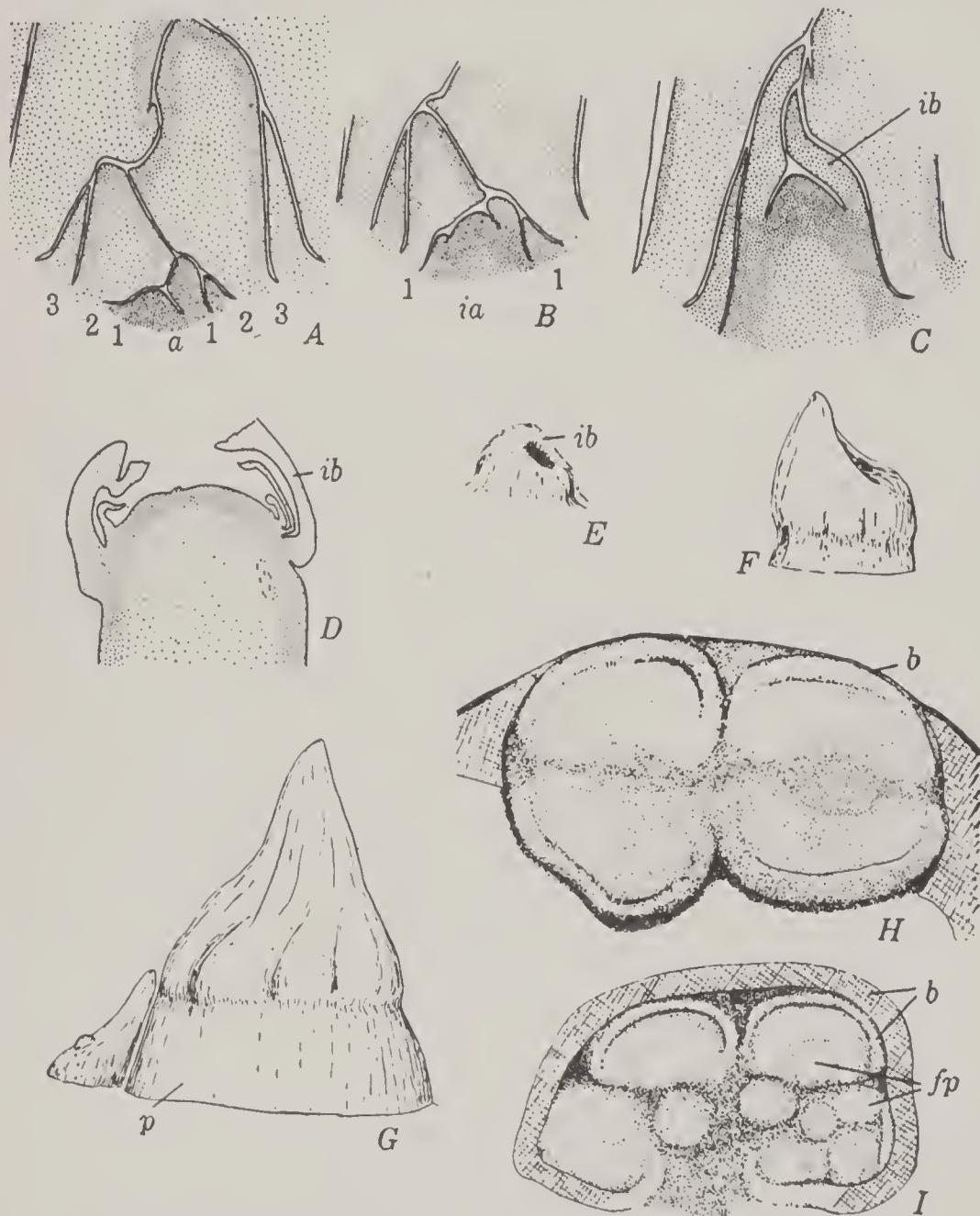


FIG. 96. Early stages in floral development. *A*, longisection through growing point of onion bulb. 1, 1; 2, 2; 3, 3 respectively are opposite portions of leaves enclosing axis *a*; *B*, primordium of axis of the inflorescence *ia* with involucral bract just arising; 1, 1 are opposite sides of the leaf enclosing it; *C*, the elongating peduncle of axis of the inflorescence showing involucral bract *ib* which completely covers the central region; *D*, apex of axis of the inflorescence somewhat flattened with additional bracts arising within involucre; *E*, axis of the inflorescence at about the stage of development as in *B*, showing unilateral development of involucre; *F*, *G*, developing flower stalks. At the base of peduncle at *p* another shoot has differentiated; *H*, within young bracts *b* are raised kidney-shaped areas from which the flowers develop; *I*, primordia of the first flowers are shown: *b*, bract; *fp*, flower primordia. The bract covering four kidney-shaped areas has been cut away. (After Jones and Emsweller, *Hilgardia*.)

stamen, which it subtends, becomes evident. In most instances, the two appear to be differentiated simultaneously from a common meristematic region, the outer portion of the primordium forming

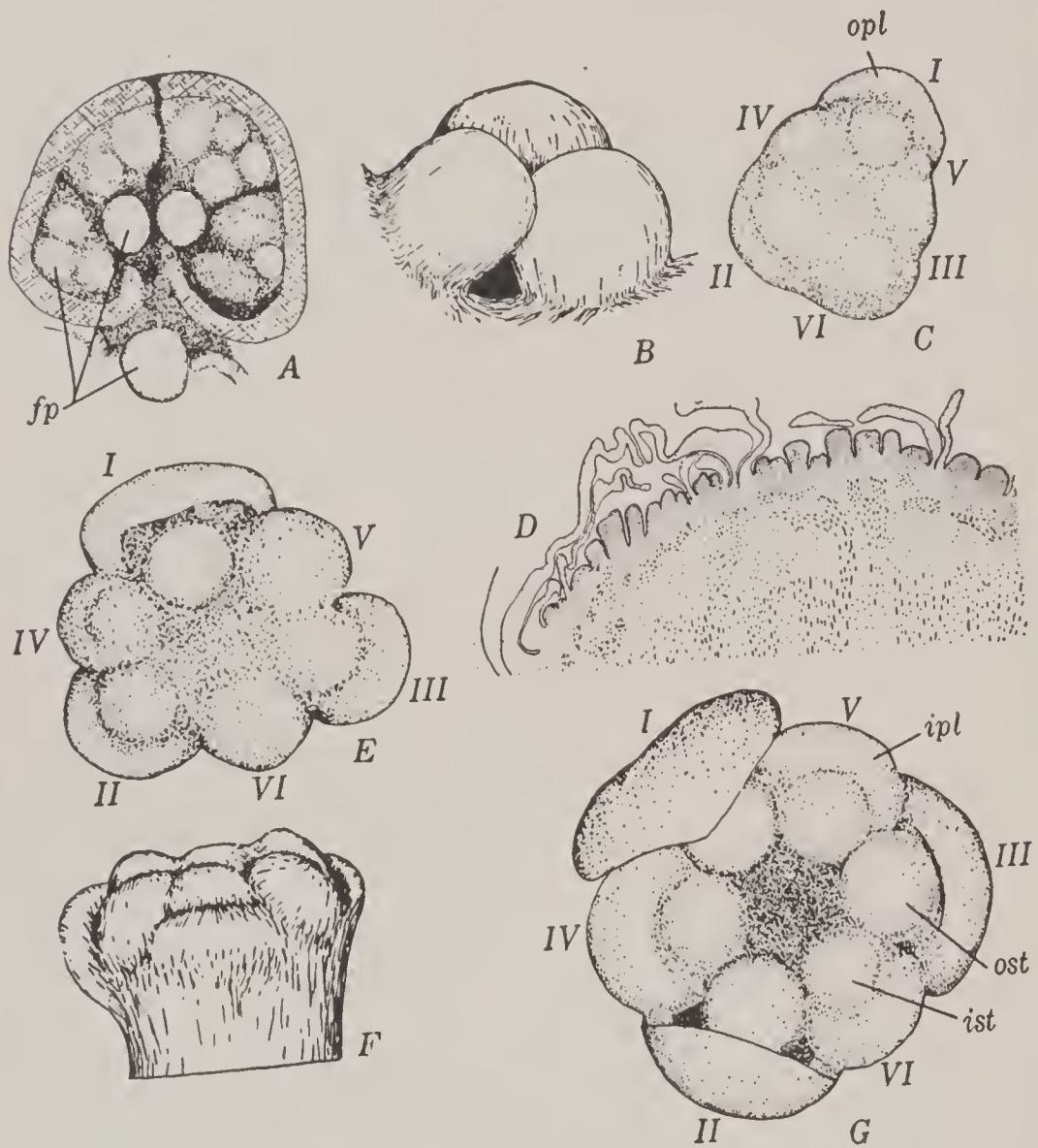


FIG. 97. *A*, a slightly older stage in floral development than in preceding figure, *I*; *fp*, flower primordia; *B*, side view of three flower primordia, *C*, top view of a young flower showing counter-clockwise differentiation of outer perianth lobes, *opl*, and outer whorl of stamens. The youngest primordium *VI* will appear opposite the oldest perianth segment *I*; *D*, longisection of a portion of inflorescence at about the time that floral organs of the oldest flowers are beginning to differentiate; *E*, top view of a young flower showing outer whorls of perianth and stamens differentiated. The inner whorls are just beginning to differentiate. Roman numerals indicate sequence of origin of different segments; *F*, side view of flower slightly younger than one shown in *E*; *G*, top view of young flower in which primordia of all perianth segments have been differentiated: *ipl*, inner perianth lobe; *ist*, inner stamen; *ost*, outer stamen. (After Jones and Emsweller, *Hilgardia*.)

the perianth segment and the inner part, one of the outer stamens. The outer perianth segments arise in a counter-clockwise direction, and the stamens follow the same order. (Fig. 97, *C*.)

The inner cycle of perianth segments, and the inner stamens which lie centrad to them, are differentiated following the formation of the outer whorls; and the first of the inner perianth segments with its stamen is formed between the oldest and second oldest of the outer whorl. (Fig. 97, E.) The second and third members of the inner cycles of perianth segments and stamens arise in sequence in a clockwise direction, although in some instances the direction is reversed. In most cases, the last segments to differentiate are opposite the oldest but "somet mes segments of the inner whorls lying both clockwise and counter-clockwise to the oldest segments of the flower appear to arise simultaneously." Although the inner stamens are differentiated later in ontogeny than the outer ones, they are the first to shed their pollen.

The carpillary primordia develop as the outer perianth segments are beginning to overarch the stamens and appear as three crescentic outgrowths which arise on the flattened meristematic surface alternate to the three inner stamens. (Fig. 98, A.) The young carpels elongate, and owing to lateral and basipetal growth, their inturned edges meet to form the three-loculed ovary of the pistil. The style is differentiated by the apical growth of the three carpels; and while the elongation of the style is taking place, the ovules arise along placenta on the inner edges of the carpels, two being formed in each locule. (Fig. 98, E-G.) Two integuments develop which surround the nucellar tissue; and by the time of anthesis, the ovule has become almost completely anatropous.

VASCULAR ANATOMY OF THE FLOWER. — At the upper limits of the flower stalk, the vascular bundles of the outer cycle anastomose so that they form a nearly continuous ring. Slightly higher, just below the divergence of the bracts which constitute the spathe, the entire vascular supply forms a complicated network of branching and anastomosing bundles from which the traces to the spathe and to the pedicels of the individual flowers diverge. Each pedicel has six vascular bundles arranged in two cycles as in the main flower stalk of the umbel. At higher levels, the pedicel becomes subtriangular, and the three outer bundles occupy positions centrad from the angles, while the three inner bundles lie slightly within the outer cycle and alternate to them. (Fig. 99, D, E.)

Each outer bundle branches, one trace supplying a segment of the outer perianth, the other the outer stamen which is subtended by this perianth segment. The inner bundles supply the inner

segments of the perianth and the inner cycle of stamens by branching in a similar manner. Each carpel has a single vascular bundle which arises as a branch from the trace that supplies the outer perianth segment and outer stamen. The point of divergence of the carpillary bundles is slightly above the level at which the outer

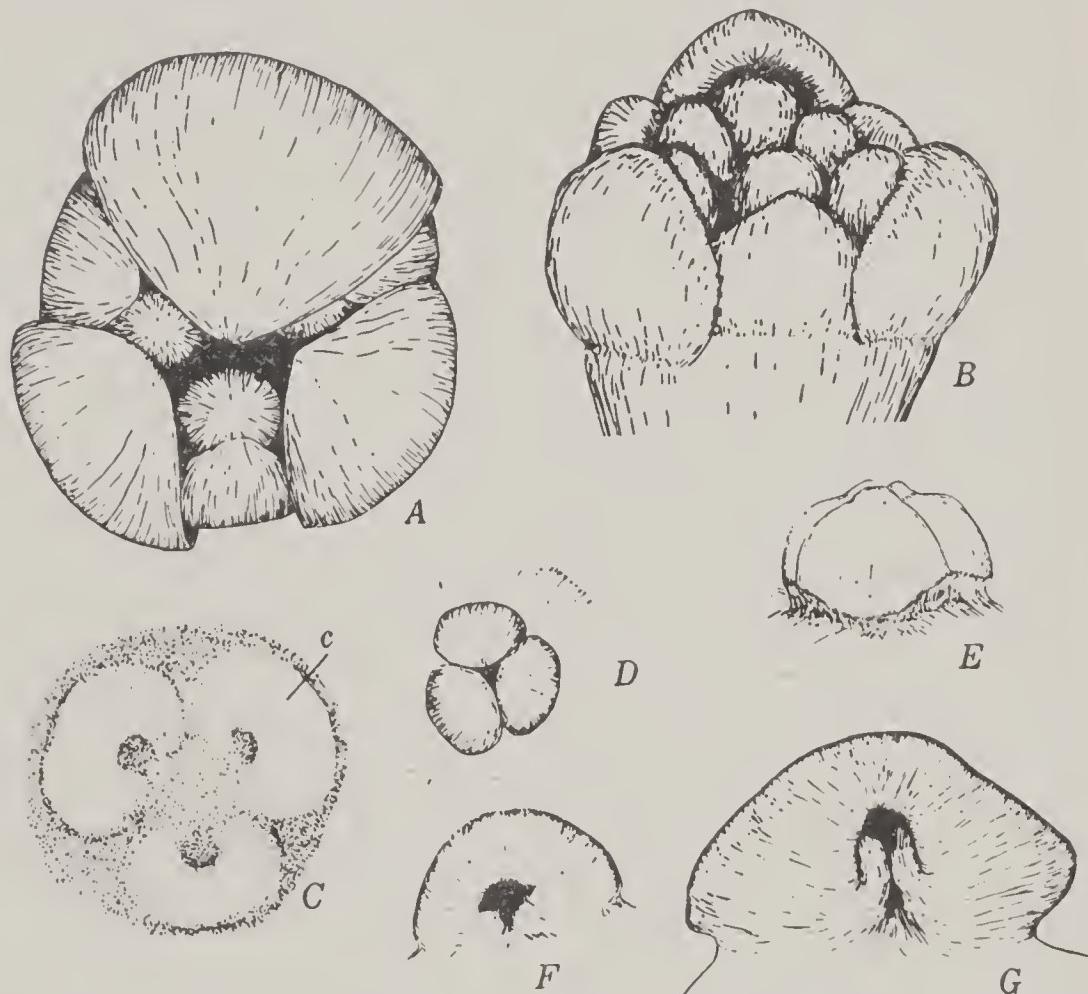


FIG. 98. A, top view of young flower in which outer perianth lobes almost cover stamens. At about this time, the carpels are differentiated; B, side view of flower slightly younger than A; C, early differentiation of the three carpels; D, carpels have grown upward until they nearly meet at center; E, carpels with the style just beginning to form; F, turned edges of single carpel showing origin of two ovules; G, a slightly older carpel than F. (After Jones and Emsweller, *Hilgardia*.)

cycle of bundles of the pedicel branch to supply the outer perianth segments and the outer stamens respectively. (Fig. 99, C.) As a result of this method of branching, each perianth segment, stamen, and carpel is supplied by one main vascular bundle. (Fig. 99, F, G.)

DEVELOPMENT OF THE MEGAGAMETOPHYTE. — Megasporogenesis and the development of the megagametophyte have been investigated for several species of Allium, including *A. Cepa*, by Weber

(22), Strasburger (18), and Jones and Emsweller (10). In megasporogenesis, the subepidermal, archesporial cell functions as the megaspore mother cell. Jones and Emsweller observed that the nucleus of the megaspore mother cell is in the prophase at about

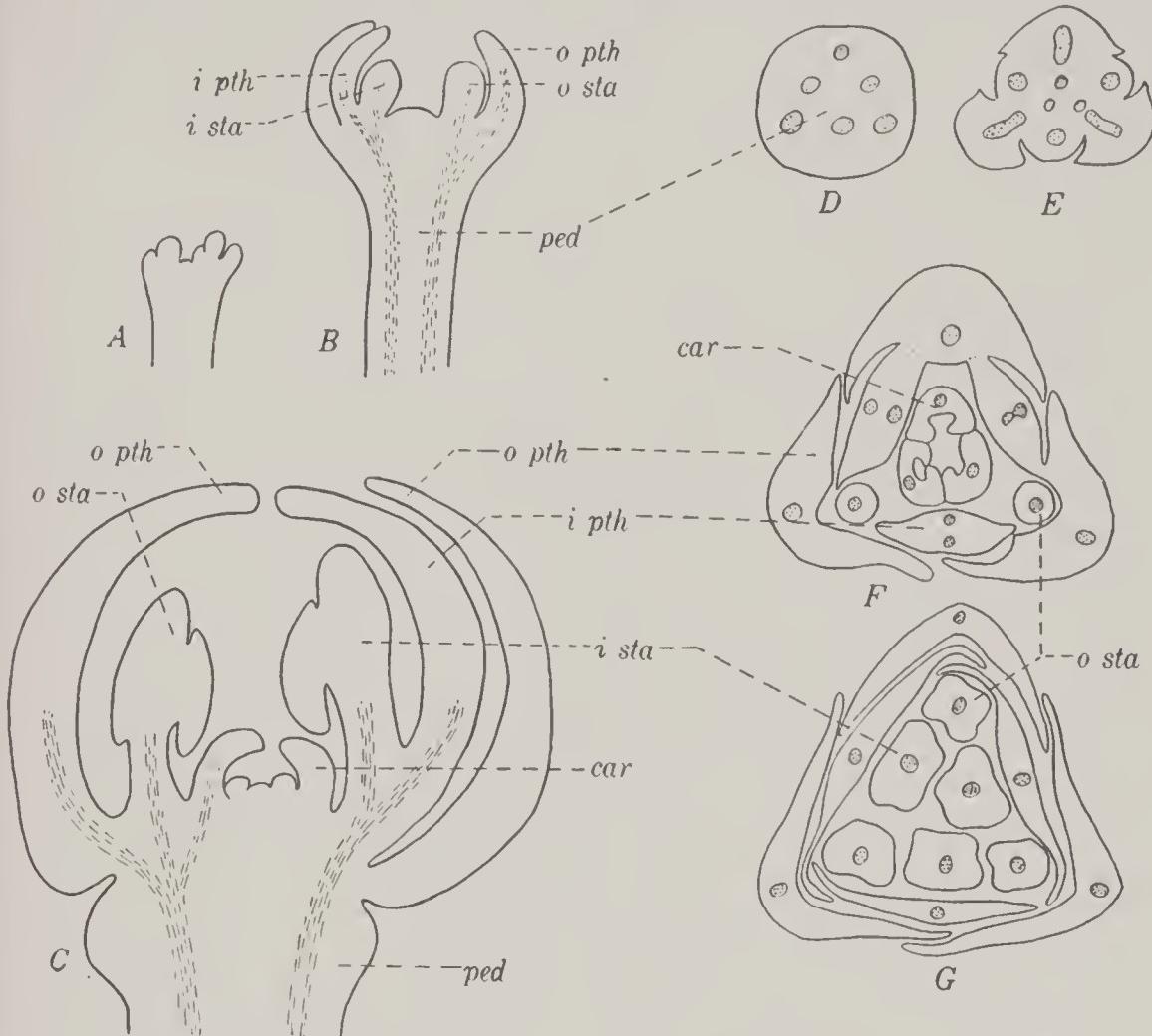


FIG. 99. *A*, longisection of young flower primordium; *B*, the same, more fully developed in which the primordia of outer perianth and stamen and inner perianth and stamen are shown; *C*, a later stage in which inner and outer stamens are well differentiated and the carpels have begun to overarch primordia of the ovules; *D*, transection of pedicel of flower showing six vascular bundles; *E*, transection at a higher level, slightly above the divergence of outer perianth segments; *F*, a transection showing outer perianth segments subtending outer stamens, inner perianth segments and undiverged inner stamens, and the three crescentic carpels; *G*, transection at a higher level showing the inner and outer perianth segments: *car*, carpel; *i pth*, inner perianth segment; *i sta*, inner stamen; *o pth*, outer perianth segment; *o sta*, outer stamen; *ped*, pedicel.

the time that the inner integument begins to differentiate. Following the first nuclear division, which is meiotic, there is a gradual disorganization of the micropylar daughter cell. This is characteristic of many of the species of *Allium*, but the formation of the megasporangia and their subsequent development appears to be variable. Porter (13) has described this stage for *A. mutabile*

Michx. and reports that the chalazal daughter cell undergoes one more division, forming two megasporangia, the inner one being functional and the micropylar one disintegrating. In *A. Cepa*, according to Jones and Emsweller, the chalazal daughter cell functions directly as the megasporangium rather than undergoing further division, and a similar situation has been described by Strasburger (18) and Weber (22) for other species of *Allium*. In species of *Allium* where both bulbils and flowers occur in the inflorescences, there may be some variations from this type of development.

In the formation of the megagametophyte, the megasporangium undergoes successive nuclear divisions to form an eight-nucleate gametophyte. The two synergids are of unequal size, the volume of the larger one being several times that of the smaller, but both are well supplied with food. In some species, the synergids disappear immediately following fertilization while in others they are more or less enlarged; and, according to Weber (22), probably act as nutritive cells until the embryo has developed to the two- or, in some instances, a several-celled stage. In *Allium Cepa*, they are probably nutritive for a short time.

EMBRYOGENY. — The development of the embryo in *Allium* has been investigated by Souèges (17) for *A. ursinum* L. and by Porter (13) for *A. mutabile* Michx. The two accounts agree in general details, and the mature embryos in each case are much like the one described by Hoffman for *A. Cepa*. The first division of the zygote is transverse, producing an apical and a basal cell. (Fig. 100, A.) This is followed by another transverse division of the basal cell, so that the three-celled embryo consists of an apical cell which is the product of the first segmentation of the egg, and an intermediate and terminal cell which result from the subsequent transverse division of the basal cell. (Fig. 100, B.) Later, oblique or vertical divisions of the apical cell give rise to the quadrants of the embryo which by further division and differentiation produce the cotyledon and growing point of the epicotyl. (Fig. 100, H, I.) Divisions of the intermediate cell produce the hypocotyledonary portions of the embryo, including the root cap, and the basal cell of the linear triad forms the suspensor by a series of divisions. As the development of the hypocotyl proceeds, a blocking off of the histogens occurs, and in the embryo there is a clearly defined plerome outside of which lies a group of meristematic cells that produce the periblem, dermatogen and the root cap. (Fig. 100, I, J.)

Polyembryony has been observed in this genus, in *A. odorum* L. Tretjakow (20), Hegelmaier (6), and Haberlandt (4) report the formation of polyembryos in this species and describe their origin from synergids, antipodal cells, and even from the inner integument of the ovule. Tretjakow found from one to three embryos derived from antipodal cells, with the zygote and some-

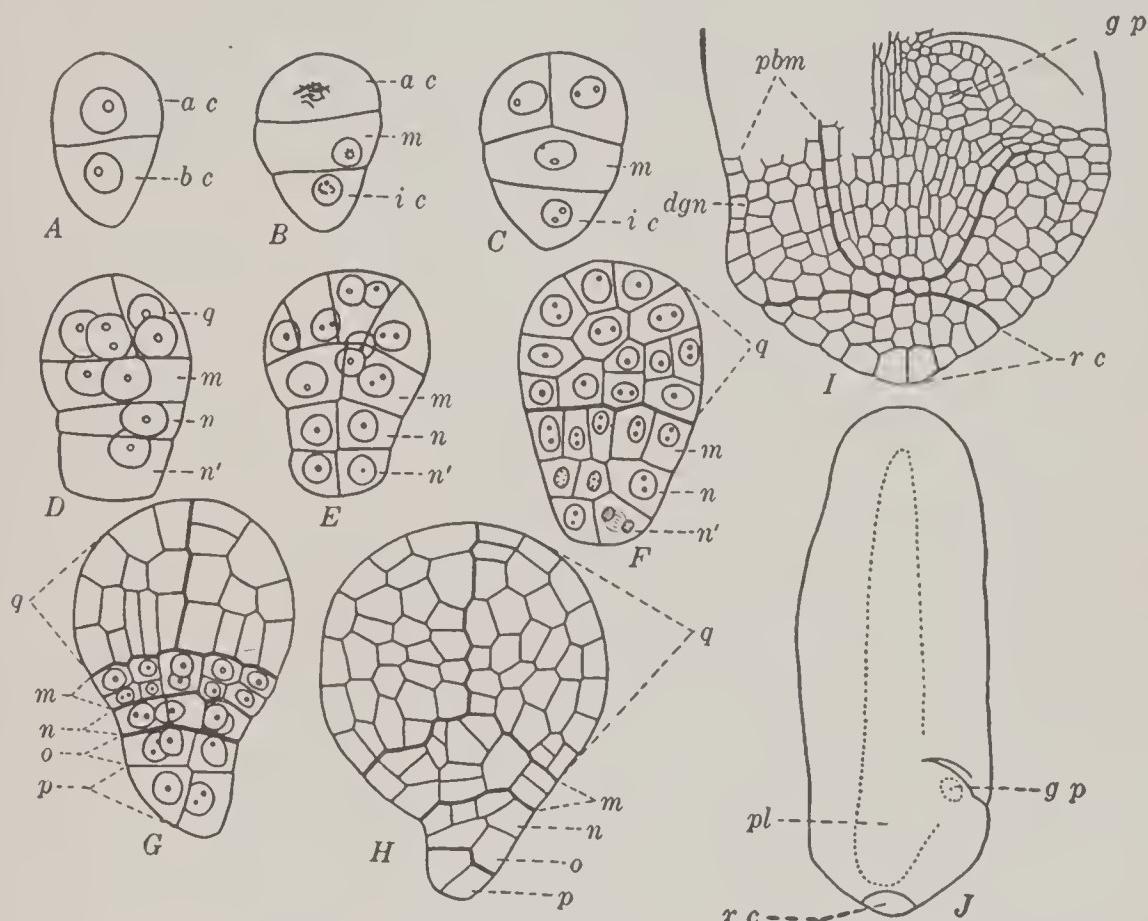


FIG. 100. *A-I*, principal stages in the embryogeny of *Allium ursinum* L., showing origin of histogens; *J*, schematic representation of embryo showing regions figured in detail in *I*: *a c*, apical cell; *b c*, basal cell; *m* and *i c*, superior and inferior cells derived from *b c*; *n* and *n'*, basal cells derived from *i c*; *o* and *p*, cells derived from *n'*; *q*, a quadrant of embryo; *dgn*, dermatogen; *g p*, growing point of stem; *pbm*, periblem; *pl*, plerome; *r c*, root cap. (Redrawn after Souèges, *Compt. Rend. Acad. Sci.*)

times the synergid forming additional embryos. Hegelmaier found as many as five embryos in a single embryo sac, one being derived from the zygote, one from the synergid, two from antipodal cells, and one from the inner integument. If the usual sequence of reduction divisions had occurred, this would result in haploid embryos, derived from the synergid and the antipodal cells; and diploid embryos from the zygote and inner integument. It appears that the embryos in investigated cases are diploid (16 chromosomes); and Haberlandt has suggested that this is the result of a

parthenogenetic development of embryos in an ovule in which no reduction division of the megasporangium mother cell occurred. If fertilization had been effected, there would be triploid embryos; and tetraploids could be formed in cases where there was also a failure of reduction division in microsporogenesis. Experiments with *A. odorum*, in which the anthers were removed and the flowers protected against fertilization, indicate that parthenogenetic development, following failure of the reduction division in the formation of the megasporangium, does occur. Under such experimental conditions, diploid embryos as described above were obtained.

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CHAPTER VIII

MORACEAE

CANNABIS SATIVA

THE true hemp plant, *Cannabis sativa* L., is cultivated chiefly for its fiber; but the seed is used for medicinal purposes, and certain varieties are grown occasionally as ornamentals. The term *hemp* has been used in connection with many plants producing bast fibers that are somewhat alike in appearance and quality, and Dodge (13) has listed 32 plants to which this common name is applied. Among these are Manila hemp, derived from the leaf stalks of *Musa textilis* Nee; Sisal hemp, secured from the leaves of species of *Agave*; Mauritius hemp, obtained from the green aloe, *Furcraea gigantea* (D. Dietr.) Vent.; and Sunn hemp, procured from *Crotalaria juncea* L.

The genus *Cannabis* is generally regarded as monotypic; but since the plant exhibits several different growth forms, it has been described under several names, and numerous varieties are recognized. It now is widely distributed, but de Candolle (8) suggested that its original habitat might have been in some region east of the Caucasus. Dewey (12) states that it was one of the earliest plants cultivated for fiber, and that its original home was probably somewhere in central Asia.

Cultivation of hemp has resulted in the development of at least three distinct types, each of which is further subdivided into varieties. One is grown in Europe, Central Asia, and the Americas specifically for the fiber; a second type is cultivated for the fruit, which is utilized as a source of oil and as a food; while the third, *Cannabis sativa*, var. *Indica* (sometimes regarded as a separate species, *Cannabis Indica*), is grown in India, Arabia, and Northern Africa for its medicinal and narcotic products. These are derived from the dried inflorescences and upper leaves of the carpellate plant, and produce alkaloids of a narcotic character which are variously known as "hashish," "ganja," and "bhang" in the

Orient. In the Western Hemisphere, especially in Mexico and southwestern United States, the drug is known as "marihuana" and is smoked in cigarettes. In many places, the species has become a most troublesome weed.

Hemp is grown for fiber in Russia and throughout Europe, especially in Italy, as well as in Africa, India, China, Japan, and to a lesser degree in Brazil and the United States. Russia produces more hemp for export purposes than all other countries, but the fiber of best quality is produced in Italy, owing in part to the manner in which the fiber is retted. The production in this country is confined chiefly to Wisconsin and Kentucky, and much of the seed used elsewhere is raised in the latter state. Hemp is also grown in Nebraska, California, Indiana, and New York.

GENERAL MORPHOLOGY

The plant is an annual and at maturity develops a rigid, woody stem ranging in height from 3 to 16 feet. The tallest forms are produced in China and Japan, where the slender, sparsely branched stalks have internodes 8 to 10 inches long. The European varieties are usually shorter with more rigid stems, and require 10 to 15 days less time to mature than do the Asiatic forms.

THE SHOOT. — The young stem is succulent, but it lignifies rapidly. At maturity, it is obtusely hexagonal, more or less grooved or furrowed; and the most common varieties in this country have a hollow stem. As Heuser (15) has pointed out, cultural conditions exert a great influence on the form of the plant, especially with respect to length of stem and degree of branching. Where the crop is not crowded, a single plant may occupy a large area, becoming much branched and attaining a bushy habit, and cases have been reported in which the main axis attained a diameter of 6 cm. or more. Such plants are undesirable for commercial fiber, and the best results are obtained when the crop is seeded thickly so that they are slender and essentially unbranched except at the tip. Under these conditions, the diameter of the stem may range from 6 to 20 mm. It is not uncommon for the lower portion of the stem to exhibit a definite curvature known as "wind-bending," which results from the pressure of prevailing winds on young plants. This and other mechanical stresses may have a detrimental effect upon the quality of the fiber produced.

The stem is leafy, but the leaves fall from the lower portions of

the axis as the plant matures. (Fig. 101.) The phyllotaxy is both opposite and alternate; and, ordinarily, the lower leaves are arranged in opposite pairs while the upper ones are alternate. Schaffner (25) has reported changes of opposite to alternate phyllotaxy as a result of rejuvenation by means of variation in the photoperiod.

The leaves are palmately compound, with from 5 to 11 leaflets, 7 to 9 being the usual number. These are rough, dark green above, somewhat lighter on the abaxial surface, linear to lanceolate and tapered at both ends, with serrate or dentate margins. They vary in length from 5 to 15 cm., are 1 to 2 cm. in width, and the petiole is 4 to 6 cm. long with persistent, pointed stipules at its base. In the leaves which subtend the inflorescences, the number of leaflets is reduced to three or even to a single large leaflet with very small awl-shaped laterals.

THE ROOT. — The root system consists of many radiating laterals arising from a primary root that extends vertically downward to a variable depth depending upon the character of the soil. Heuser (15) has observed



FIG. 101. Left, carpellate hemp plant; right, staminate plant held up for comparison. (Reproduced from Yearbook of U. S. Dept. of Agriculture, 1913.)

that roots may penetrate to a depth of 2 meters in well-cultivated soil with a permeable subsoil; but where the plants grow in a heavy humus soil, the main tap root seldom reaches a depth in excess of 30 to 40 cm. The horizontal spread of the lateral roots also depends to a large degree upon the soil type. In mineral soils, where the primary root penetrates deeply, the laterals arise chiefly from the upper 20 to 40 cm. of the axis, and the largest of

them may have a lateral spread of 80 cm. In the richer humus soils where the main tap root penetrates less deeply, numerous lateral roots are formed in the upper 10 to 20 cm. of the soil; and the root system is much more compact.

THE INFLORESCENCES. — Hemp is dioecious, and the number of staminate and pistillate plants is relatively constant under normal conditions, the number of the former being somewhat less than that of the latter. Associated with the dioecious condition is a distinct vegetative dimorphism which has been described by McPhee (22). The staminate plants are taller and more slender than the carpellate, and the terminal staminate inflorescences have few leaves. The carpellate plants are shorter and more stocky, with a broad crown of leaves associated with the terminal inflorescence. (Figs. 102 and 103.)

Although hemp is dioecious, it is not uncommon for an individual plant to bear both staminate and carpellate flowers. According to McPhee (22), the occurrence of monoecious plants is more common when the daily exposure to light is short; and under experimental conditions, it has been possible to modify and control to some degree the production of staminate and carpellate flowers. This does not seem to affect the vegetative characters, which remain the same regardless of whether the plant is strictly dioecious, or later becomes monoecious through the production of both staminate and carpellate flowers. Schaffner (26), as a result of rejuvenation experiments, has reported that "sex reversal can be successfully brought about during the second ontogenetic differentiation cycle of rejuvenated plants in individuals that were of pure sex expression in the first or natural differentiation cycle"; and has suggested that "speculations as to the nature and fixity of sex, especially in relation to heredity, are of questionable value, and formulae based arbitrarily on the behavior of individuals during



FIG. 102. Habit of staminate flowers of hemp.
(Reproduced from *Yearbook of U. S. Dept. of Agriculture*, 1913.)

their first differentiation cycle are not to be accepted as an explanation of the real nature of such individuals." On the other hand, McPhee (23) notes that "sex determination in hemp can be explained on a genetic basis, and that the inheritance is of the XY type."

THE STAMINATE INFLORESCENCE AND FLOWER. — The stamine flowers develop in small, drooping, branched panicles, which



FIG. 103. Habit of carpellate flowers of hemp. (Reproduced from *Yearbook of U. S. Dept. of Agriculture*, 1913.)

arise in the axils of foliage leaves. (Figs. 102 and 104, A.) The flowers of the panicle may occur singly on slender pedicels or in groups, and usually the terminal branches bear three flowers, a median one and two laterals which are subtended by bracts or stipules. (Fig. 104, B.) The individual flowers are apetalous with a deeply parted calyx having five greenish-yellow or red lobes that are widespread at maturity. There are five stamens, and the anthers are suspended from long thread-like filaments. (Fig. 104, C.) The plants are wind pollinated, and large numbers of

white, spherical, papillate pollen grains are liberated through terminal pores.

The oval sepals are acuminate, the outer surface and margins being covered with multicellular glands and slender, pointed, unicellular hairs with crystals of calcium oxalate deposited in their swollen bases. The inner epidermis is practically devoid of hairs and stomata which are present in the outer epidermis. Except in the region of the median vein, the mesophyll is spongy

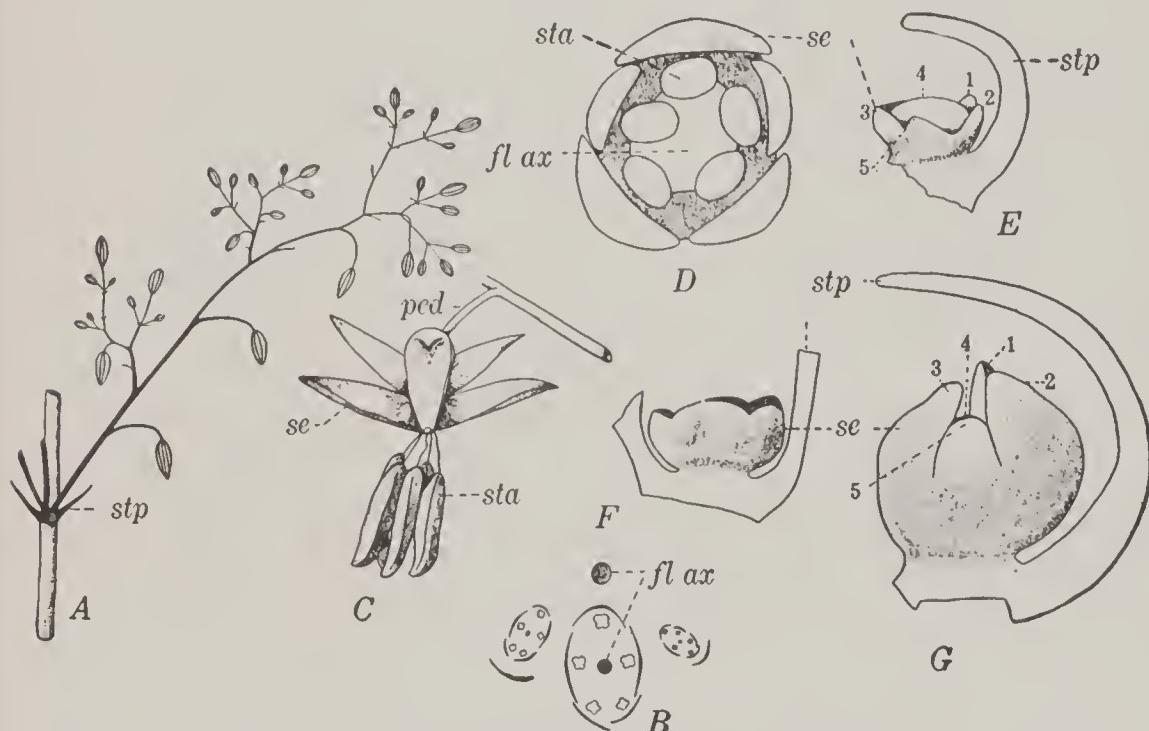


FIG. 104. A, diagrammatic representation of staminate inflorescence; B, diagram of branch of staminate inflorescence showing three flowers; C, habit of staminate flower; D, face view of young flower, showing arrangement of parts; E, F, and G, successive stages in development of staminate flower. The numerals indicate the sequence of origin of sepals: fl ax, floral axis; ped, pedicel; se, sepal; sta, stamen; stp, stipule. (Redrawn and adapted from Briosi and Tognini, *Istituto Botanico di Pavia*.)

and one to two cells in thickness; but at the margins, mesophyll is lacking and the sepal consists of only the epidermal layers. As the sepal matures, the inner epidermis becomes much stretched and crushed.

In the ontogeny of the staminate flower, the conical floral primordium which commonly develops in the axil of a stipule first produces the five cone-shaped initials of the sepals. These arise in a definite succession; the first two are adjacent to the stipule, the third one develops opposite to the stipule, and is followed by two laterally placed ones. (Fig. 104, E, F, G.) After the differ-

entiation of the sepal primordia, the five staminal primordia arise, each one being opposite a sepal. (Fig. 104, D.)

THE CARPELLATE INFLORESCENCE AND FLOWER. — The carpellate flowers are borne in short spikes on a more or less compact bushy and leafy shoot. (Fig. 103.) The flowers are closely aggregated at the apex of the inflorescence and are produced in pairs in the axil of a leaf, each flower being subtended by a stipule. (Fig. 105, B.) Commonly one of each pair of flowers is abortive. A short branch

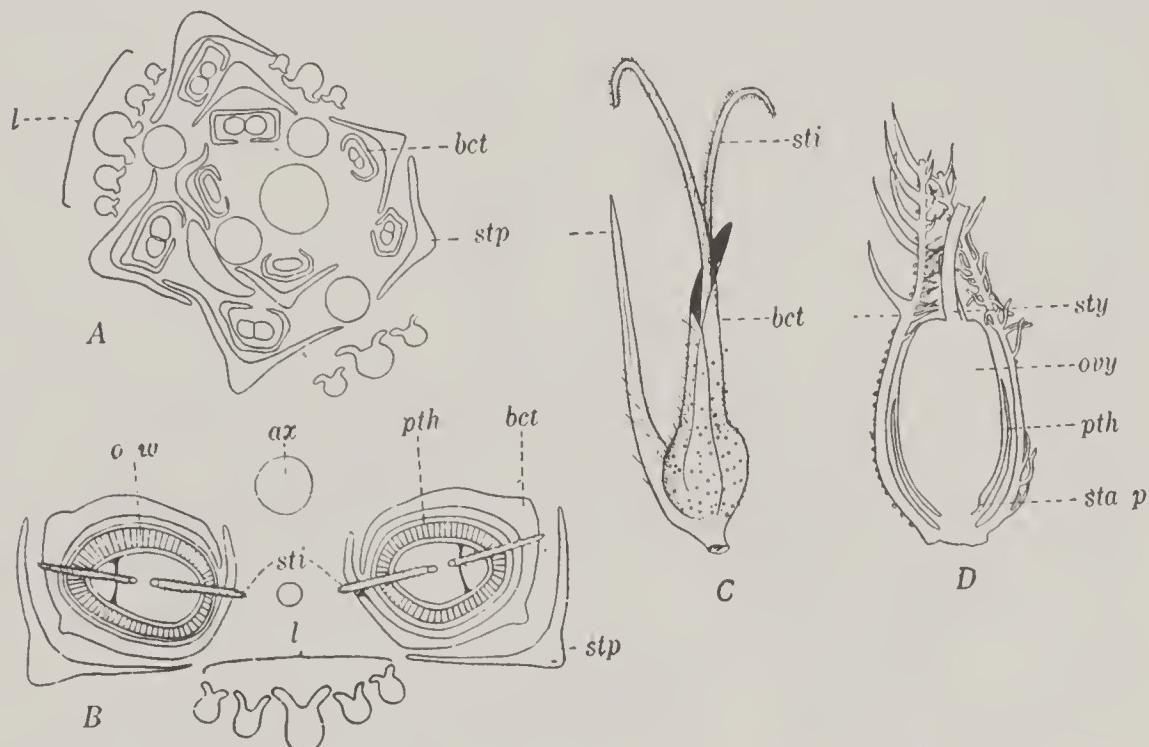


FIG. 105. A, transection of apex of carpellate inflorescence, showing arrangement of leaves, stipules, bracts, and flowers; B, diagram of branch of carpellate inflorescence, showing a pair of flowers; C, habit of single carpellate flower; D, longitudinal diagram of carpellate flower, showing floral parts: *ax*, floral axis; *bct*, floral bract; *l*, leaf; *ovy*, ovary; *ow*, ovary wall; *pth*, perianth; *sta p*, staminal primordium; *sti*, stigma; *stp*, stipule; *sty*, style. (Redrawn and adapted from Brioso and Tognini, *Istituto Botanico di Pavia*.)

which arises in the axil of the leaf subtending the pair of flowers bears another leaf with stipules and flowers, and this in turn produces an axillary branch of the third order. (Fig. 105, A.) Since the branches are short, this type of branching results in the formation of the compact carpellate inflorescence. The leaves which subtend the paired flowers tend to be in a $\frac{2}{5}$ phyllotaxy rather than the decussate arrangement of the lower portion of the vegetative axis.

The carpellate flower is relatively simple in structure, consisting of a pistil surrounded by a transparent, more or less papery perianth. (Fig. 105, C.) In its normal position, the green scabrous floral

bract with its overlapping edges completely surrounds the mature flower except for the exserted stigmas. It is conical, open at the top, terminated by a pointed beak; and, when uncurled and expanded, heart-shaped and acuminate. The abaxial surface of the bract is thickly covered with glands and glandular emergences that are intermixed with large, stout, conical hairs. (Fig. 105, D.) The adaxial surface is without glands, and hairs are seldom present except at the margin and near the apex of the bract where the inner surface is more exposed. The bracts are several cells in thickness at the median line, and the spongy mesophyll is chlorophyllose. The projecting emergences of the abaxial surface which are terminated by glands contain compact chlorenchymatous cells at their bases. The multicellular glands are derived from epidermal cells and consist of a stalk and a terminal cap or plate. The stalk may be a single or multicellular row of cells, and the expanded terminal portion consists of several cells over which a very thick cuticle is formed.

The perianth is continuous and entire, forming a cup-like structure with a smooth or slightly fringed margin which at maturity covers about two-thirds of the ovary. (Fig. 106, H.) It develops as a definitely diverged structure free from the ovary but becomes closely adherent as the ovary enlarges. (Fig. 106, D.) The perianth is a simple hyaline membrane consisting of the two epidermal layers between which are a few spongy mesophyll cells; and at its base, a network of small vascular bundles extends through the mesophyll. The cells of the abaxial epidermis are elongated in the direction of the long axis of the ovary; and, rarely, long unicellular hairs may be produced. The adaxial surface resembles the abaxial but is devoid of hairs, and neither epidermis contains stomata. The mesophyll is comprised of transparent, thin-walled cells that are homogeneous and non-chlorophyllose, and it seldom exceeds three or four cell layers in thickness.

The pistil consists of an oval, unilocular ovary, which is slightly flattened and somewhat depressed at its stylar end, and two stylar branches and stigmas. The styles are cylindrical, and the papillate stigmas are divaricate with their apices curved outward and downward. (Fig. 105, C.)

According to Briosi and Tognini (6) the primordium of the carpellate flower originates as a dome-shaped structure in the axil of a foliar bract or stipule. (Fig. 106, A, B.) At the base of the

flower, there is a floral bract which later encloses the other floral parts. The ovary wall arises as a ring-like fold at the base of the floral primordium, and gradually encloses its apex. (Fig. 106, C.) When the ovary wall has completely overgrown the floral axis, two opposing points on its margin begin to grow more rapidly, initiating the two styles and stigmas. (Fig. 106, E, F.) The

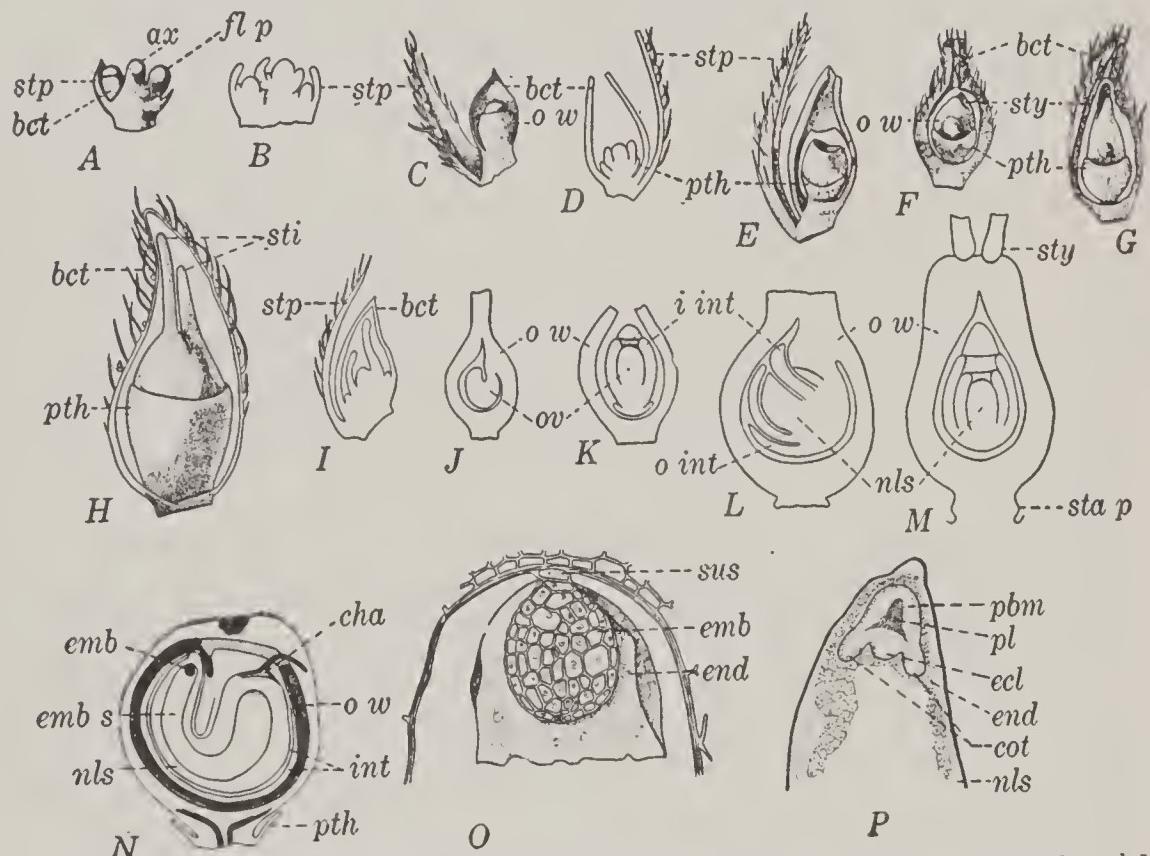


FIG. 106. A-M, stages in floral development of carpellate flower: A, C, E, F, G, and H, habit drawings of successive stages; B, D, I, J, and L, diagrammatic longisections showing relation of floral parts at successive stages; K, face view of a stage somewhat more developed than J; M, face view, at stage about the age of L; N-P, stages in development of embryo: ax, vegetative axis; bct, floral bract; cha, chalaza; cot, cotyledons; ecl, epicotyl; emb, embryo; emb s, embryo sac; end, endosperm; fl p, floral primordium; int, integuments; pth, perianth; sus, suspensor. (Redrawn and adapted from Briosi and Tognini, *Istituto Botanico di Pavia*.)

styles elongate unequally, and one is always somewhat longer than the other even at maturity. (Figs. 106, G, H, and 105, C.) Within the ovary, the remaining tissue of the primordium forms the nucellus and finally a single ovule is developed which becomes completely campylotropous with a curved megagametophyte. (Fig. 106, J, M, N.)

Shortly after the initiation of the carpillary wall, a second fold of tissue arises at the base of the primordium, growing up and

around the carpel until it encloses approximately two-thirds of it. (Fig. 106, D-H.) This becomes the membranous perianth described above. Briosi and Tognini observed knob-like projections at the base of the ovary and above the perianth, and interpreted them as being rudimentary primordia of stamens that become arrested in development. (Figs. 105, D, and 106, M.)

Zinger's (31) account of the ontogeny of the carpellate flower is at variance with the above in respect to the development and character of the perianth. In most of the varieties of hemp which he examined, there were two distinct perianth primordia. The first primordium appears at the base of the floral axis on the side toward the floral bract, while the second develops on the dorsal side of the floral axis at a higher level than the first. Both may appear somewhat late in ontogeny, so that they are not perceptible until the carpillary primordia are differentiated. In most instances, the primordium on the side toward the floral bract persists as a small protuberance without further development; and this is sometimes the case with the posterior primordium, so that there may be no perianth when the fruit is mature. When the posterior primordium develops, it forms a thin, round or elliptical scale-like structure which lies on the dorsal side of the ovary. Zinger found a perianth completely enclosing the basal portion of the ovary in two horticultural varieties which he designated as *Cannabis gigantea* Hort. and *C. himalayana* Hort.

At the base of the nucellus, the inner and outer integuments arise in that order, the inner one at first exceeding the outer in rate of growth, but ultimately being overgrown and enclosed by it. (Fig. 106, K, L, M.) As noted by Zinger, the massive inner integument becomes completely coalescent with the thick outer one, and covers the apex of the nucellus in such a way that the micropylar canal becomes entirely closed by the integumentary tissue. Following pollination, the pollen tube either grows through the tissue which fills the micropyle or pierces the two integuments; and, upon reaching the nucellus, it branches about its apex, finally sending a single branch into the megagametophyte.

EMBRYOGENY. — Following fertilization, the transverse segmentation of the zygote produces the suspensor and embryo proper. The suspensor never becomes elongate, remaining as a short stalk of one or two cells. (Fig. 106, O.) The embryo is at first globular but there is an early differentiation of the cotyledons which develop

as lateral lobes on either side of the growing point of the epicotyl. (Fig. 106, *P.*)

Concurrent with the development of the embryo, an abundant endosperm is formed which fills the embryo sac. This is gradually utilized by the embryo, which develops a curvature corresponding to the contour of the embryo sac. Some of the endosperm still remains in the seed at maturity, surrounding the embryo and occupying the region between the primary root and the cotyledons. (Fig. 108, *A.*) Twin embryos have been reported by Savelli (24).

HISTOLOGY OF THE FRUIT AND SEED. — The fruit is an akene which is light brown to dark gray, or in some cases mottled. It is smooth, somewhat compressed, and orbicular or oval in form; but varies in this respect and in size, as does the enclosed seed. Heuser (15) reports the average length of the pointed types as 4.3 mm., with diameters ranging from 2.75 to 3.3 mm.; and Dewey (12) records the length of the fruit as from 3 to 6 mm. with diameters of from 2.5 to 4 mm.

The "seed" of commerce is actually the fruit which in some cases comes into the market enclosed within its hooded floral bract. (Fig. 107, *A.*) The outer epidermis of the floral bract is characterized by its hairs and glands. The hairs attain a length of 0.5 to 1.0 mm. and taper abruptly or gradually to a pointed apex from spherical bases which contain cystoliths of calcium oxalate. The globular gland consists of eight or more cells radiating from two central ones which may be sessile; but, in most cases, they are borne on many-celled stalks. (Fig. 107, *D.*) The secretory cavity is formed by the separation of the outer cuticle from the terminal cells.

The pericarp of the fruit, which is comprised of five distinct regions, has been described by Winton (29). The outermost zone, or epicarp, is a layer of sclerenchymatous cells which are sinuous in outline as seen in surface view. Their radial walls are only slightly thickened in some regions; while, in others, they are so thick that the lumen of the cell is much reduced. All the walls of this layer are porous. The second region of spongy parenchyma consists of one or more layers of colorless cells between which there are many intercellular spaces. Numerous anastomosing bundles, that can be seen through the epicarp, extend throughout this layer, which is thicker along the two keels of the fruit. (Fig. 107, *B.*) Underlying the hypodermal layers are the brown

cells which form the third zone. These derive their name from the brown contents, and can be distinguished from the hypodermal cells by the thick walls and color. The fourth layer consists of the dwarf cells, which are small, colorless, and porous, with

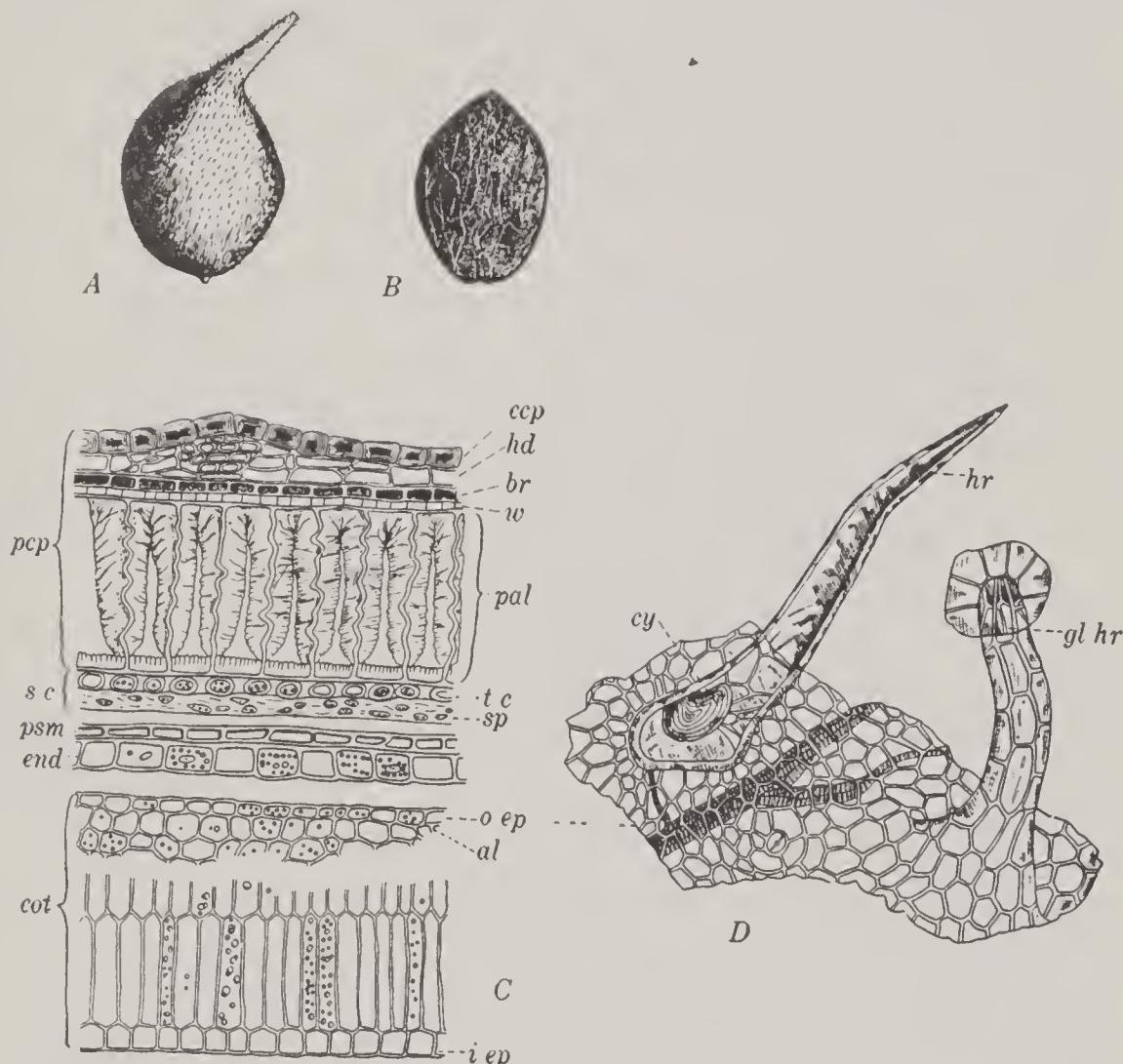


FIG. 107. A, hemp fruit enclosed by persistent floral bract; B, outer surface of fruit with bract removed; C, transection through section of fruit coat, seed coat and cotyledon; D, surface view of portion of floral bract showing two types of epidermal hairs arising from it: *al*, aleurone grains; *br*, brown cells; *cot*, cotyledon; *cy*, cystolith; *ecp*, epicarp; *end*, endosperm; *gl hr*, glandular hair; *hd*, hypodermis; *hr*, non-glandular hair; *i ep*, inner (adaxial) epidermis of cotyledon; *o ep* (left), outer (abaxial) epidermis of cotyledon; *o ep* (right), outer epidermis of floral bract; *pal*, palisade cells of pericarp; *pcp*, pericarp; *psm*, perisperm; *sc*, seed coat; *sp*, spongy parenchyma of seed coat; *tc*, tube cells; *w*, dwarf cells. (Redrawn and adapted by permission from *Structure and Composition of Foods*, by Winton and Winton, John Wiley and Sons, Inc.)

sinuous radial walls. Because of their extreme thinness, they can be seen in transections only in carefully prepared material. The innermost zone of the pericarp is the conspicuous palisade layer. The outer and radial walls of the palisade cells are so greatly thickened that the lumen is reduced to a narrow line for nearly two-

thirds of the length of the cell; but, near the inner tangential wall, the radial walls are abruptly narrowed so that the lumen is wide. The inner wall is porous and moderately thickened. (Fig. 107, C.)

The green seed coat consists of two layers. The outermost one is comprised of tube cells which are distinct from the inner layer owing to their elongated form and the extended intercellular spaces. The inner layer consists of spongy parenchymatous cells that are somewhat irregular in outline. In the mature fruit, the perisperm and endosperm are each one cell layer in thickness and adhere to each other; but, in a soaked fruit, they may be readily separated from the seed coat and the embryo. The endosperm also extends between the cotyledons and hypocotyl as a membrane several layers in thickness. The cells of the endosperm contain protein grains resembling the aleurone grains of cereals.

The embryo, which is curved so that its axis is U-shaped, consists of two plano-convex cotyledons enclosing a well-developed epicotyl, a subcylindrical hypocotyl, and primary root. The epidermal layers of the cotyledons are composed of small cells containing aleurone grains. Beneath the abaxial epidermis are several layers of isodiametric cells, and underlying the adaxial one are two or more layers of palisade cells. (Fig. 107, C.) The orientation of the embryo is such that the tip of the primary root and the apices of the cotyledons are directed toward the micropylar (chalazal) end of the seed, and the stylar end of the ovary. (Fig. 108, A.)

DEVELOPMENT OF THE SEEDLING. — Upon germination, the primary root emerges from the fruit coat at the stylar end, splitting the coat into halves which remain united at the base, enclosing the cotyledons until they are pulled above the ground by hypocotyledonary growth. (Fig. 109.) The primary tap root grows very rapidly; and, under favorable conditions, may reach a length of 7.5 to 10.0 cm. within a period of 48 hours after emergence. This rapid rate of elongation is then retarded; and, as early as the third or fourth day, there is a marked development of lateral roots which arise just below the soil surface. At this time, the hypocotyl is also elongating and becomes erect. The epicotyl is pubescent and oval in transection, increasing slightly in diameter toward the cotyledonary node. The expansion of the cotyledons is rapid after they become free from the fruit coat; and, according to Lubbock (20), they are approximately equal in width but differ in length,

the longer one being 1.4 to 1.6 cm., the shorter 1.0 to 1.3 cm. long. The cotyledons function both as photosynthetic and storage organs for 15 to 20 days, when they become discolored, shrivel, and finally fall.

The cotyledons are obovate to spatulate, taper toward their bases, and the terminal portions are somewhat recurved. They are sessile and connate at the base, forming a cotyledonary collar. The venation consists of a prominent midrib with two lateral veins arising from its base which unite with two others that originate

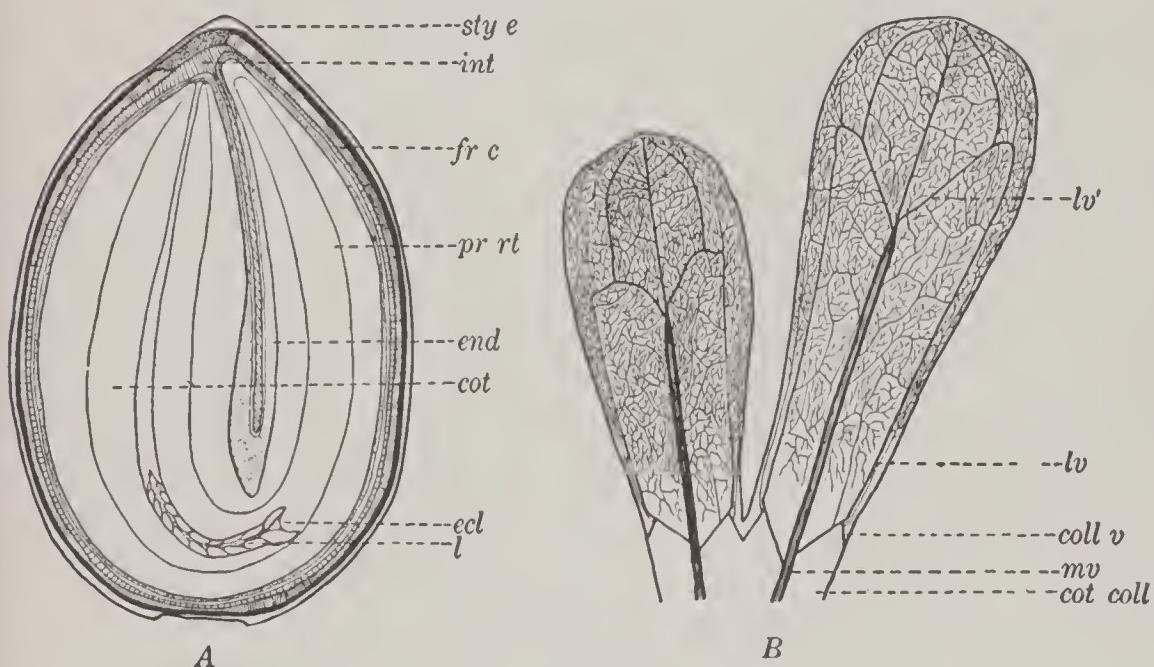


FIG. 108. A, median longisection of fruit cut perpendicular to cotyledonary plane; B, diagram of cotyledonary collar showing venation. The collar has been cut open in intercotyledonary plane and the cotyledons spread with abaxial surface up: *coll v*, collar vein; *cot*, cotyledon; *cot coll*, cotyledonary collar; *ecl*, epicotyl; *end*, endodermis; *fr c*, fruit coat; *int*, integument; *l*, leaf; *lv*, primary lateral vein; *lv'*, secondary lateral vein; *mv*, midvein; *pr rt*, primary root; *sty e*, stylar end. (After Berkman.)

from the midvein at about the midpoint of the cotyledon and extend to the apex. (Fig. 108, B.) The lamina of the cotyledon is thicker and more spongy than that of the first foliage leaves. The mesophyll is chlorophyllose, consisting of two or three layers of palisade cells which occupy the adaxial half of the leaf, and as many as ten or more layers of spongy parenchyma may develop in the abaxial portion. Stomata occur with about equal frequency in the upper and lower epidermal layers, and both surfaces produce unicellular hairs. The cells of the adaxial epidermis have sinuous walls, except where they overlie the median vein, while those of the abaxial surface are rectangular with straight walls.

During the first week or ten days of seedling development, while the hypocotyl is obtaining its maximum length of 5 to 6 cm., the epicotyl elongates rather slowly. Later, the rate of epicotyledonary growth is accelerated; and, according to Berkman (3), the first internode reaches its normal length of 3 to 5 cm. by the twelfth or thirteenth day. The first pair of foliage leaves above the cotyledons are simple and ovate with serrate margins, and are functional for a short time only. In most instances, the second and third pairs are digitate, the former usually having three leaflets and the latter four or five. The leaflets above the third pair are as described under general morphology.

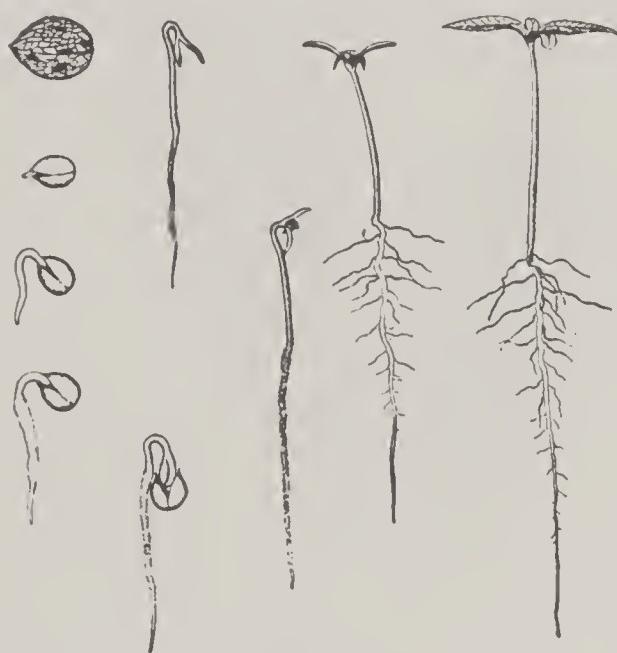


FIG. 109. The fruit and stages in development of seedling.

THE PRIMARY ROOT.—The root is diarch, with two groups of primary phloem flanking the primary xylem strand. The protoxylem abuts the pericycle, which is multiseriate, consisting of four or more layers lying centrad to the endodermis. In the intercotyledonary plane, it is usually only two layers in width. The endodermis is uniseriate and Caspary strips begin to

differentiate at about the time that the metaxylem matures, but they do not become well developed until secondary thickening is initiated. The cortex is composed of five to seven concentric layers of parenchymatous cells with prominent intercellular spaces. The outermost layer forms a distinct hypodermis which is similar in structure to the epidermis except that it produces no root hairs. (Fig. 110, A.) The root has a blunt cone-shaped root cap.

There are several accounts of the structure and ontogeny of the root, and these do not agree in all respects. Van Tieghem and Douliot (28) described the pericycle as a single layer of cells, and also interpreted the periblem as one layer of initials. Flahault (14), Briosi and Tognini (7), and Berkman (3) report the periblem as consisting of two layers of initials, and the pericyclic layer as soon becoming multiseriate as a result of periclinal divisions.

In the ontogeny of the root, the primary structures are derived from three well-defined histogens which are similar to those described by Janczewski (16) and Crooks (9) for the primary root of *Linum usitatissimum*. The root cap and epidermis are derived from a common layer of initials designated as the calyptrogen-dermatogen. The cortical tissue originates from the two-layered periblem, and the stelar tissues are derived from the plerome.

The development of the root cap and epidermis from the calyptrogen-dermatogen layer results from the differential character of the

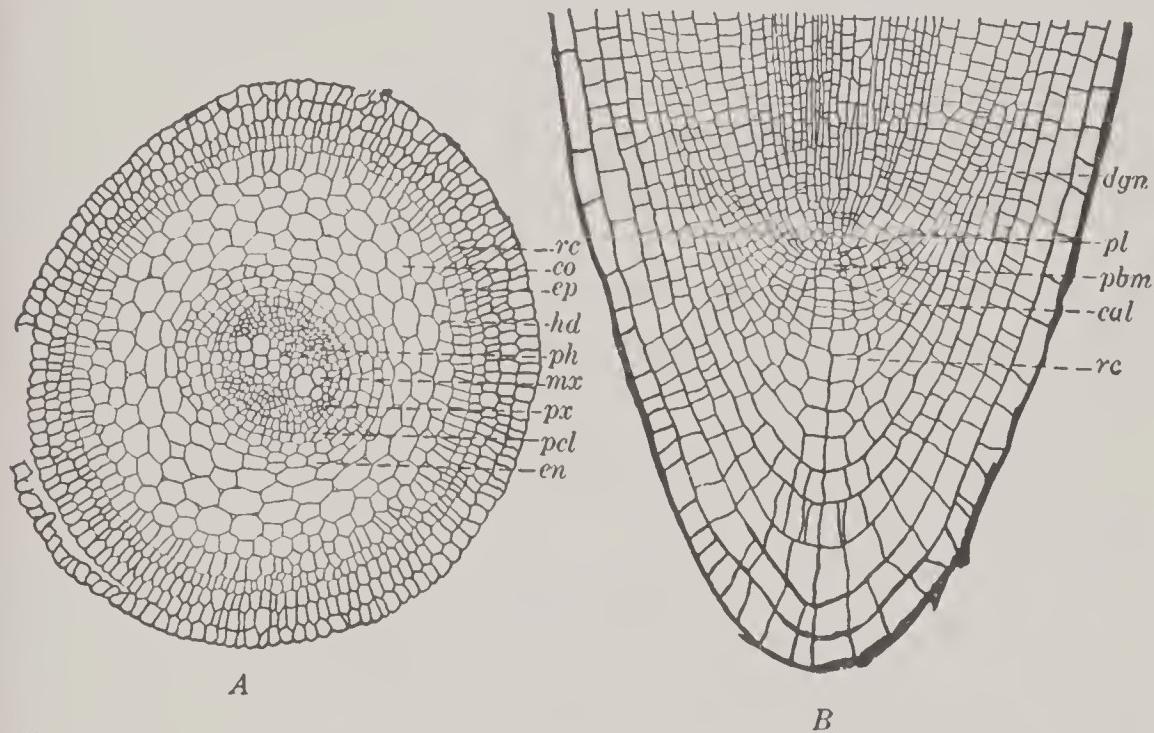


FIG. 110. A, transection of primary root 0.6 mm. above root tip; B, median longisection of root apex showing histogens in detail: *cal*, calyptrogen; *co*, cortex; *dgn*, dermatogen; *en*, endodermis; *ep*, epidermis; *hd*, hypodermis; *mx*, metaxylem; *pbm*, periblem; *pcl*, pericycle; *pb*, phloem; *pl*, plerome; *px*, protoxylem; *rc*, root cap. (After Berkman.)

division of its cells. The cells of this layer which immediately overlie the periblem at the tip of the root divide periclinally to form the root cap cells. The more laterally placed ones divide anticlinally, and function as a true dermatogen in producing the epidermis. The manner in which the root cap and dermatogen arise from the dual histogen has been described by de Bary (2):

"The divisions of the initial layer, which are parallel to the surface of the bluntly conical apex, add on the one hand new cells to the root-cap above the apex, and on the other hand renew the initial layer itself. As the distance increases from the apex of the periblem, which by its growth in length is constantly advancing, the divisions become rarer, and at last cease. The last of these separates the initial cell

into two, one of which is added to the root-cap, the other to the dermatogen as a permanent member of it. . . . The cells of the dermatogen and root-cap, which owe their origin to the division just described, divide further by walls perpendicular to the surface; from each therefore is produced a section of a layer consisting of several or many cells."

The cells of the root cap, which later become oriented in a lateral position because of the elongation of the root axis, may divide anticlinally. In this manner, they compensate for the growth in length of the root axis, and each series of root cap cells keeps pace with the elongation of the root axis until the layer of which they are a part becomes the outermost one and disintegrates. The cells of the calyptra which form the terminal vertical rows of the cap do not usually undergo further division, except for one or two cells which are proximal to the calyptrogen; but they enlarge in all three dimensions until they are two or three times the size of the calyptrogen initials. As a result of the anticlinal divisions of the lateral rows of the calyptrogen and the concurrent enlargement of the cells in the vertical rows, the root cap consists of a very regular series of cell layers which overlie one another. (Fig. 110, B.)

The cortex is derived from the two-layered periblem which forms a terminal cap over the small group of plerome cells at the root apex. The outer layer of the periblem divides only in anticlinal planes, in this manner giving rise to the outermost cortical layer which becomes the hypodermis. The initials of the inner layer divide in all planes to produce the four- to seven-layered parenchymatous portion of the cortex and the endodermis.

The pericycle is the first tissue of the stele to differentiate and is derived from the outermost layer of the plerome. The pericyclic cells can be identified early in ontogeny by their dense contents and greater axial dimension as compared with adjacent cortical cells. Following the differentiation of the pericycle, the primary phloem and xylem develop simultaneously. The protophloem is comprised of elongated parenchymatous cells with relatively small diameters. The primary phloem ducts are formed by the breakdown of a linear row of cells adjacent to the pericycle, as many as three or four occurring in each phloem group. They are completely differentiated at a level approximately 1.5 cm. above the root tip, and the number may increase until there are seven or more in each

primary phloem group by the time that secondary growth is initiated. The ducts are ephemeral; and, together with other elements of the protophloem, become crushed against the pericycle as secondary growth proceeds.

Of the primary xylem, three to five thin-walled annular and spiral elements constitute each protoxylem point. The outermost and smallest of these abuts the inner layer of the pericycle, which is three or four cells in width by the time the first annular vessel is mature. The other protoxylem elements are bounded laterally by regions of fundamental parenchyma in which cambial activity is later initiated. The metaxylem elements continue to mature centripetally so that the primary xylem strand is complete at a level about 0.6 mm. above the root tip. The metaxylem vessels have distinctly bordered pits in which the borders are narrow and the torus thin. Scalariform vessels may rarely occur.

A rather unusual case of tetraploidy in the primary root has been reported by de Litardière (19) and Breslawetz (5). The diploid number of chromosomes in hemp is 20 and this obtains for the cells in the plerome, but both investigators found the tetraploid number of 40 in the cells of the periblem. This situation was observed by de Litardière in specimens selected from two varieties of hemp grown in different localities; and, coupled with the confirmatory report of Breslawetz (5), would indicate that the condition is general rather than aberrant. Several explanations have been advanced to account for it. Breslawetz attributes it to the occurrence of nuclear divisions in the cells of the periblem which are not followed by cylogenesis, but, instead, by the enlargement of the cells involved and by the fusion of the two nuclei in each cell. On the other hand, de Litardière did not encounter any binucleate cells, and suggests that the situation may arise from a normal metaphase followed by a monocentric telophase which would produce a single tetraploid daughter nucleus. This same phenomenon has also been reported by de Litardière (18) and Langlet (17) for *Spinacia*. The latter, however, did not agree with de Litardière in respect to *Cannabis sativa*, as he found tetraploid cells abundant in all tissues of its root tip.

THE FORMATION OF LATERAL Roots. — The primordia of lateral roots arise early in the ontogeny of the primary root at about the time the protoxylem begins to mature. As a result of divisions of the pericyclic cells in three planes, conical growing points are

differentiated in roots that are less than forty-eight hours old. The endodermis of the primary axis persists as a continuous layer over the lateral root primordium until it is well differentiated and has reached the outer limits of the cortex. The point of origin of the lateral roots is approximately on the same radius as the protoxylem strands; and, according to van Tieghem and Douliot (28), the axis of the new root usually deviates 15° to 20° from this plane. The ontogeny of the lateral root is similar to that of the primary root, and this is also true of adventitious roots which may arise in the hypocotyl.

VASCULAR TRANSITION. — The structure of the hypocotyl is root-like from the ground level to a point about 1.5 cm. below the cotyledonary node, except that the central portion of the axis becomes parenchymatous. This condition begins about a millimeter above the ground level, where the central portion of the axis is comprised of sclerenchymatous cells rather than metaxylem. At successively higher levels, the cells of the central parenchyma have thinner walls, and immediately below the cotyledonary node there may be a complete disintegration of the pith in plants that are not more than two weeks old.

The character of the metaxylem elements also changes, these being differentiated with spiral thickenings in the upper hypocotyl; and vessels with bordered pits, such as occur in the metaxylem of the root are rarely found. The pericycle is multilayered as in the root, the number of layers ranging from three to five outside the protoxylem points, with two layers in the intercotyledonary plane. The endodermis is not clearly defined, and the cortex of seven or more layers is limited outwardly by a definite hypodermis.

The first modification of the root-like organization of the stelar tissue occurs about 1.5 cm. below the cotyledonary node where the metaxylem is differentiated tangentially with reference to the protoxylem points. This results in the formation of two V-shaped groups of primary xylem in which the protoxylem occupies the apex of the V and the metaxylem the extended arms. Each phloem group lies adjacent to one of the lateral metaxylem groups, and this relationship is maintained throughout the entire transition region.

As the reorientation of the metaxylem proceeds, a vascular strand is diverged from each arm of metaxylem toward the intercotyledonary plane; and the two strands on either side of the inter-

cotyledonary plane so derived converge at a slightly higher level, forming the vascular bundles that supply the first epicotyledonary leaves. As maturation of the tangentially oriented metaxylem and the epicotyledonary bundles proceeds, the pericycle becomes active, resulting in a slight increase in the diameter of the hypocotyl from this point up to the cotyledonary node. At the same time, there is a differentiation of a large number of resin or latex ducts in the phloem of the epicotyledonary bundles. As the metaxylem is differentiated in a more and more tangential position, it finally assumes a position with relation to the protoxylem so that the two arms of the metaxylem are extended at right angles to the cotyledonary plane. This orientation occurs slightly below or at the cotyledonary node, the protoxylem lying between two groups of metaxylem and in a line with them. In this manner, the double bundle of the midvein of the cotyledon is formed.

In most instances, the primary xylem is definitely endarch at the base of the cotyledon, but the protoxylem is separated from the metaxylem by parenchymatous tissue. This relationship persists to a point just above the middle of the cotyledon, where the protoxylem and two metaxylem groups converge to form a single bundle. At the base of the cotyledon, the midvein branches, giving off a lateral endarch bundle on each side, one being diverged at a slightly higher level than the other; and these lateral strands in turn are branched to form two principal veins. In each case, the divergent branch which is directed toward the apex of the cotyledon becomes a primary lateral vein. (Fig. 111.) The other branch descends to meet a similar one of the opposite cotyledon, and the two meet at a point somewhat lower than their point of divergence. This results in the formation of a continuous V-shaped strand which lies in the intercotyledonary plane of the cotyledonary collar. (Fig. 112.)

THE STEM. — The fiber of commerce is derived from the stem; and, in consequence, its structure has been studied extensively by textile engineers. Dewey (11) has described the ideal plant as one which attains a height of 10 to 12 feet, is $\frac{1}{4}$ to $\frac{3}{8}$ of an inch in diameter at the base, and develops internodes 10 inches or more in length. The stem should be prominently fluted, with a comparatively large central pith cavity so that it forms a hollow cylinder that is more easily broken by retting, since in this type, the fiber is generally tougher.

The young stem is more or less grooved and ridged, owing to the development of the principal bundles and the longitudinal strands of collenchyma. (Fig. 113.) These are arranged in a ring

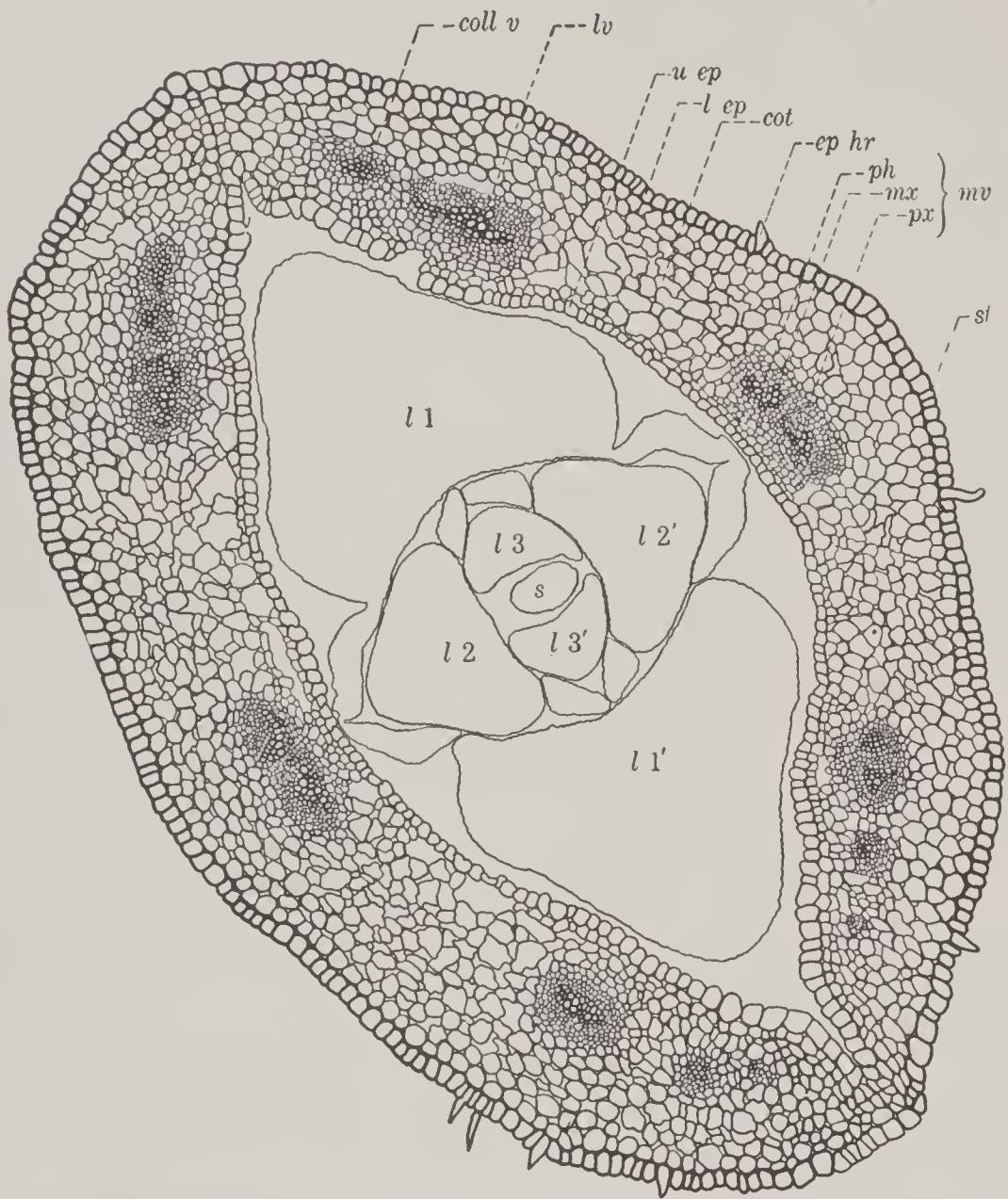


FIG. 111. Transection of cotyledons near their bases and enclosed apex of shoot: *coll v*—collar vein; *cot*, cotyledon; *ep br*, epidermal hair; *l 1-l 1'*, first pair of foliage leaves; *l 2-l 2'*, second pair; *l 3-l 3'*, third pair; *l ep*, lower epidermis; *lv*, lateral vein; *mv*, midvein; *mx*, metaxylem; *ph*, phloem; *px*, protoxylem; *s*, stem tip; *st*, stoma; *u ep*, upper epidermis. (After Berkman.)

and are separated from one another by medullary rays which are later occluded when an interfascicular cambium develops and secondary thickening is begun.

The epidermis is somewhat cutinized, producing numerous hairs and glands. The pointed non-glandular hairs are unicellular and

develop from a raised base so that when they break off, a warty circular scar remains. Cystoliths are formed in their bases as in the epidermal hairs produced on the leaves and floral bracts. The glandular hairs are multicellular and resemble those described for the floral bract. Stomata are not produced in large numbers,

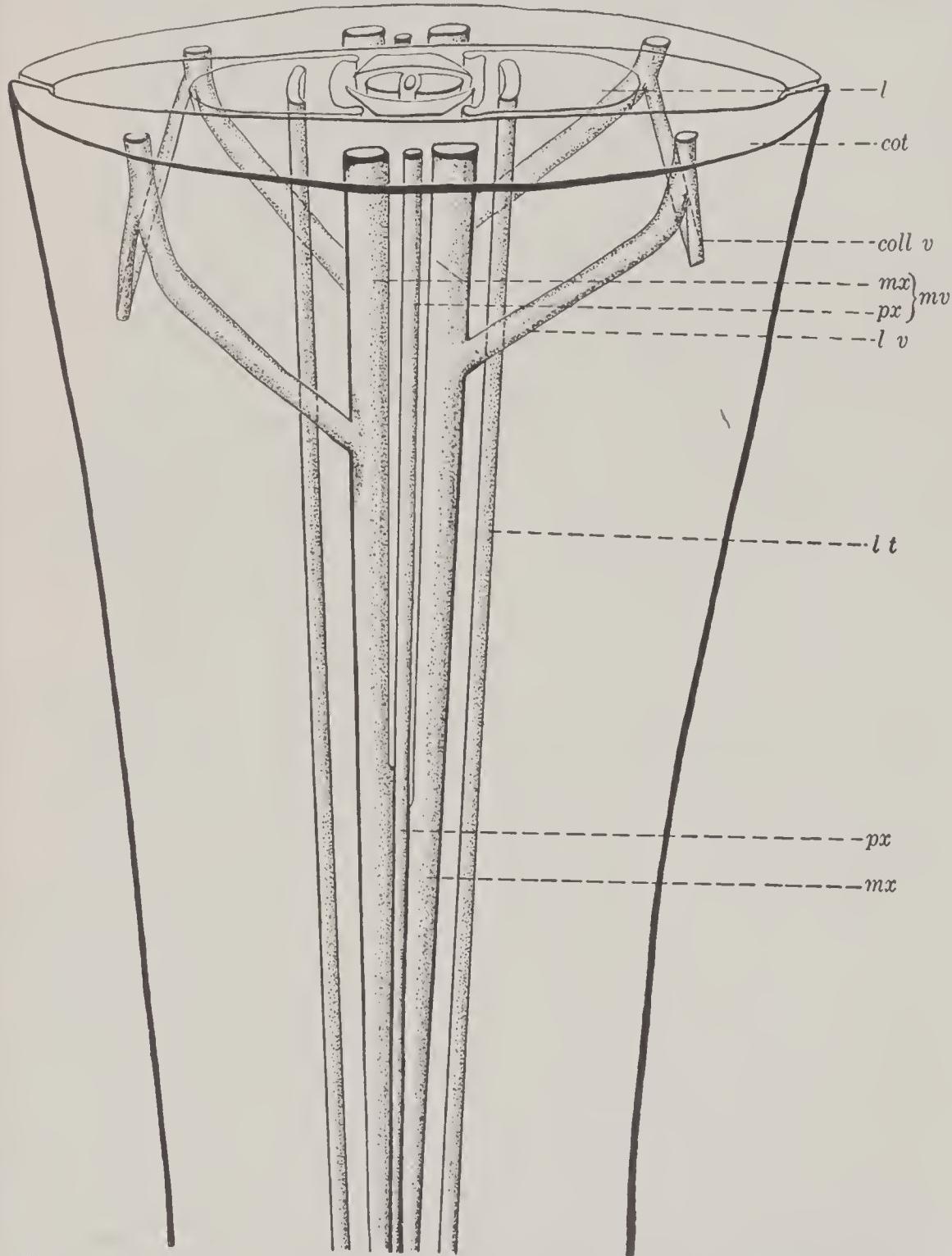


FIG. 112. Schematic diagram of vascular system of hypocotyl showing transition: *coll v*, collar vein; *cot*, cotyledon; *l*, leaf; *l v*, lateral veins; *l t*, leaf trace; *mv*, midvein; *mx*, metaxylem; *px*, protoxylem. (After Berkman.)

and, according to Heuser (15), their frequency is only 12 per square centimeter as compared with approximately 3000 per square centimeter in flax. Briosi and Tognini (7) reported a frequency of 5 per square millimeter in a young stem 2 mm. in diameter, pointing out that the frequency per unit area diminishes greatly as the stem matures. The radial and tangential diameters of the epidermal

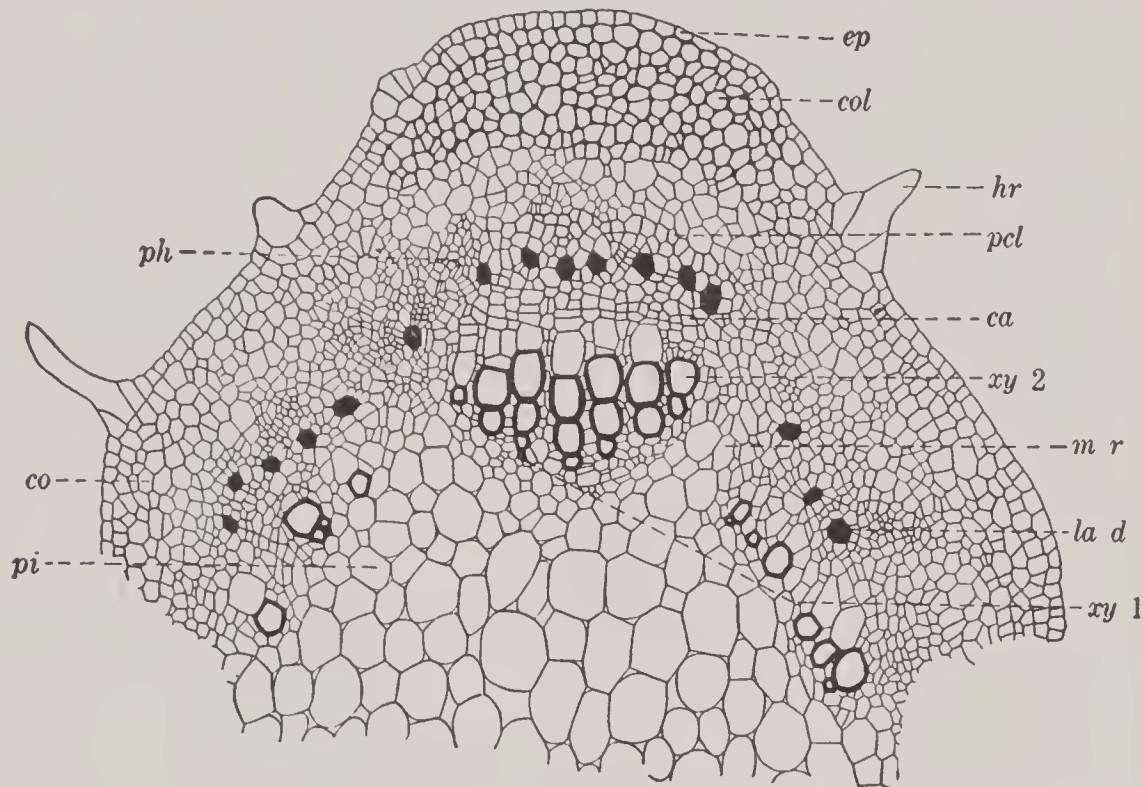


FIG. 113. Transection of portion of young stem: *ca*, cambium; *co*, cortex; *col*, collenchyma; *ep*, epidermis; *hr*, epidermal hair; *la d*, latex or resin duct; *mr*, medullary ray; *pcl*, pericycle; *ph*, phloem; *pi*, pith; *xy 1*, primary xylem; *xy 2*, secondary xylem.

cells are approximately equal, and they are three to four times as long as broad.

Adjacent to the epidermis is a zone of chlorenchyma, two or three cells in width, which extends completely around the periphery of the stem including the ridges where it separates the collenchyma from the epidermis. The chlorenchymatous cells form a compact zone at first; but, later in ontogeny, they become considerably stretched tangentially and large intercellular spaces develop. The cells of the hypodermal layer are larger than the others, and also become thicker-walled as maturation proceeds. Within the zone of chlorenchyma, strands of thick-walled, compact collenchymatous cells form a part of the ridges of the stem. The cortical zone is not wide; and, aside from the chlorenchyma and collenchyma, there are only a few layers of parenchymatous cells. (Fig. 114.)

As the stem develops, the pericycle forms a multilayered region in which the fibers are developed. These cells can be recognized in

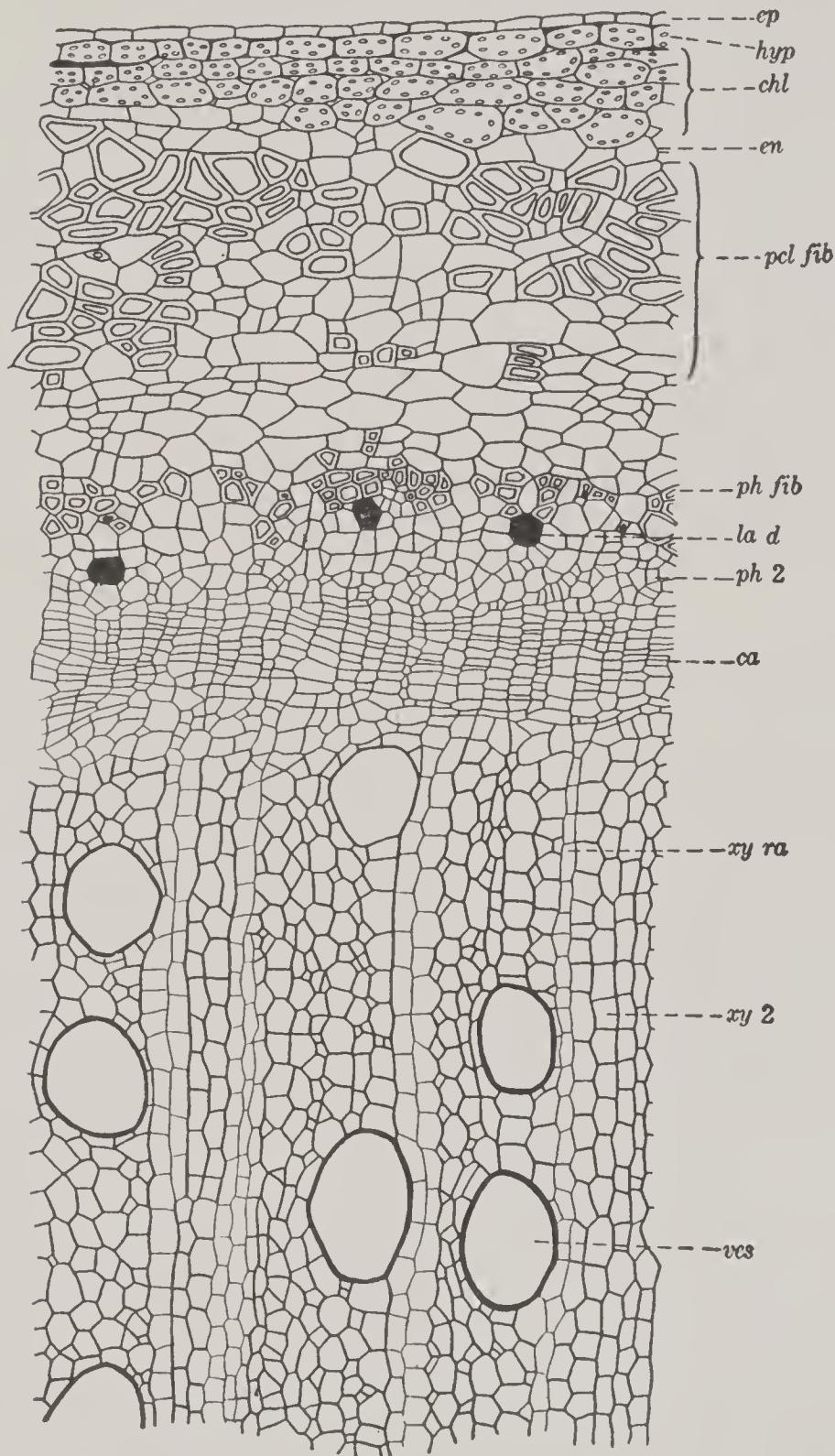


FIG. 114. A sector of transection of nearly mature stem showing development of pericyclic and phloem fibers: *ca*, cambium; *chl*, chlorenchyma; *en*, endodermis; *ep*, epidermis; *hyp*, hypodermis; *la d*, latex duct; *pcl fib*, pericyclic fibers; *ph fib*, phloem fibers; *ph 2*, secondary phloem; *ves*, vessel; *xy ra*, xylem ray; *xy 2*, secondary xylem. The primary xylem, pith, and central cavity are not shown.

the transection of a relatively young stem, since they form a definite zone of angular cells lying between the phloem and the cortical region. Their development and characteristics are described in a succeeding section.

The collateral vascular bundles are separated from one another by medullary rays. The number of primary bundles varies at different stem levels, owing to branching and anastomoses, and to variation from a $\frac{2}{5}$ spiral to a decussate phyllotaxy. Briosi and Tognini (7) have discussed the course and number of bundles of the stem axis beginning in the hypocotyl. By successive branchings, the hypocotyledonary bundles are increased from 2 to 4, 8, and 12, then reduced by anastomoses to 10. Of these, four comprise the cotyledonary traces and enter the cotyledons at the cotyledonary node. In succeeding internodes, the number of primary bundles ranges from 12 to 16, depending upon the location of the transection examined in relation to a node. Three bundles supply each leaf.

The primary xylem consists of annular, spiral, reticulate, or pitted vessels. These are differentiated in radial rows, each usually consisting of a single series of progressively larger protoxylem and metaxylem elements that are separated from those of adjacent rows by parenchymatous ray tissue. As secondary thickening proceeds, the development of interfascicular cambium forms a continuous cylinder, and there is an extensive production of xylem fibers, parenchyma, large vessels, and ray parenchyma. Where two vessels lie in direct contact with each other, they are interconnected with bordered pits, and simple ones occur in walls separating the vessels from xylem parenchyma and ray cells. The xylem rays are one or two cells in width, consisting of thin-walled parenchymatous cells whose radial dimensions slightly exceed the tangential ones, and which are approximately twice as high as broad. The elongated, tapered xylem fibers do not attain great length and they are not pitted. A single fiber usually does not exceed 0.5 mm., and the uniformity in length is very striking.

The phloem consists of sieve tubes, companion cells, parenchyma, fibers, and latex or resin ducts. The sieve tubes have clearly defined sieve plates that are either transverse or oblique, and they can be readily distinguished from the ducts by this characteristic. The companion cells are slender and taper to a point where the sieve plate of the adjacent sieve tube is somewhat larger in diameter

than the caliber of the remainder of the tube. The phloem fibers are smaller, shorter, thinner-walled, and more brittle than the pericyclic fibers. They occur in zones in the phloem, either singly or in groups. In the older portions of the stem, continued secondary thickening may result in the formation of successive zones of fibers, giving the phloem a banded appearance.

The ducts are apparently unique for the Moraceae, as they differ from the unsegmented types found in the Asclepiadaceae and Euphorbiaceae in being unbranched, and in their manner and point of origin. They are also unlike the latex vessels of Papavaraceae, Cariaceae, and Musaceae, since they are not formed from a longitudinal series of cells by the absorption of their end walls. Zander (30) has described the structure and development of the ducts in detail, and notes that they are unbranched, unicellular, and multi-nucleate. They do not occur in the root, cotyledons, or greater part of the hypocotyl; and are not similar in their ontogeny to the primary phloem ducts found in the primary root.

In ontogeny, the ducts first appear at the time of the differentiation of the first leaves above the cotyledons. They occur in the primary phloem of the median bundle of the leaf, and are differentiated downward through the cotyledonary node and into the upper portion of the hypocotyledonary axis. Additional latex ducts arise in the same manner at the tips of the vegetative axes as the subsequent leaves are differentiated. (Fig. 115.) The initials of the latex ducts are round or oval when first distinguishable in the growing point and in the leaf primordia. The lumen of the duct is larger than that of the adjacent cells and the cell wall is somewhat thicker. They contain a golden-brown granular substance and have spindle-shaped nuclei that are larger than the subspherical nuclei of the adjacent parenchymatous cells.

As the leaf and axis develop, the latex ducts become long, sinuous, unsegmented canals which may attain an extraordinary length. Zander observed ducts which extended through more than one internode of a mature plant exceeding 30 cm. in length. In no instance was there any indication of either branching or anastomosing, and he concluded that each one was an independent structure. They occur in the outer limits of the primary phloem, and the number of ducts in transections of stems, varying in age from very young seedlings up to mature plants over 3 meters in height, reveal no significant differences. Zander concluded from this that

there is no production of additional ducts as a result of secondary thickening.

The pith consists of large thin-walled cells with intercellular spaces, and prior to the disintegration of the centrally located ones, they contain numerous crystals of calcium oxalate. Similar crystals occur in the parenchymatous cells of the cortex, pericycle, and phloem.

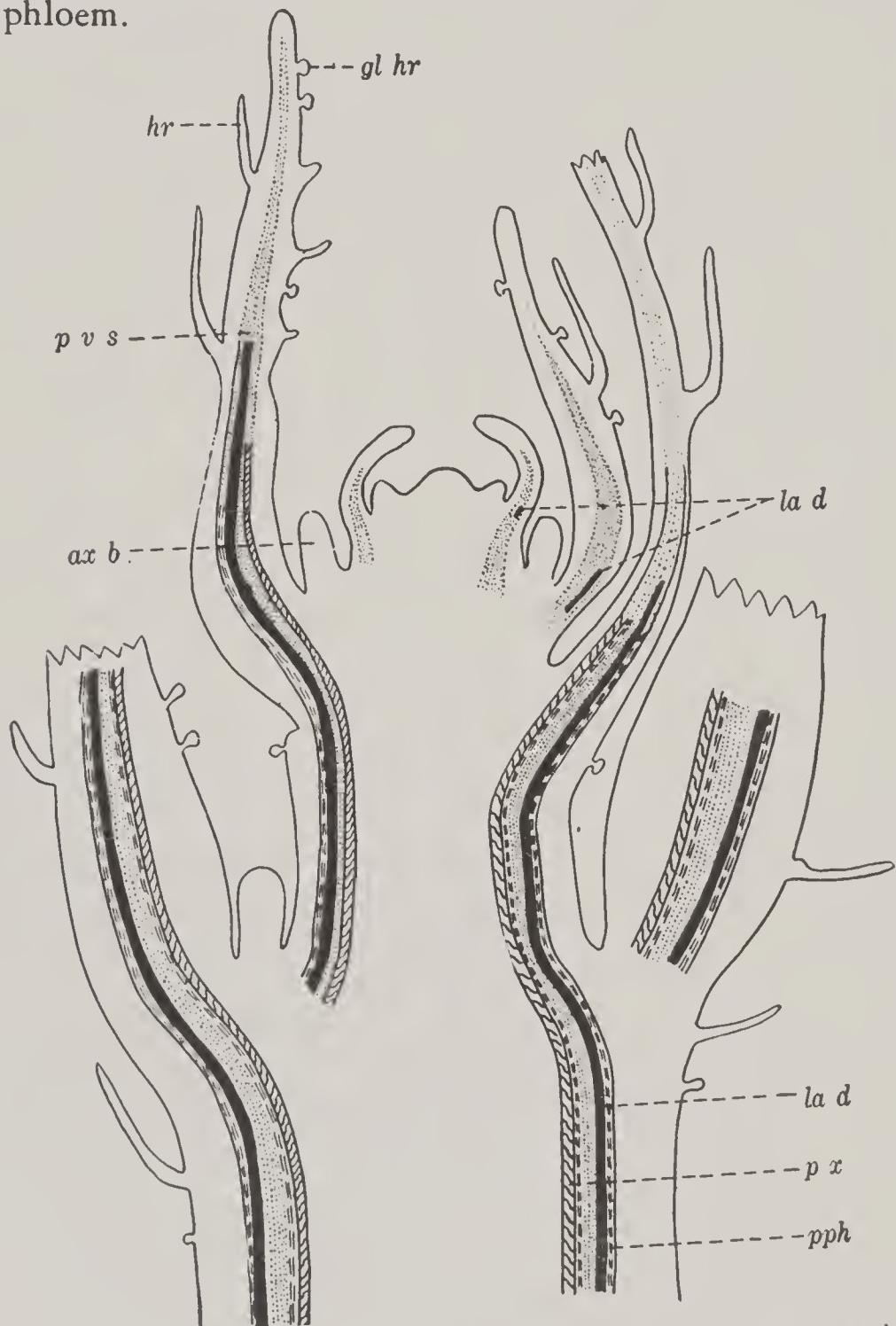


FIG. 115. Median longisection of apex of vegetative axis showing origin of latex ducts in young leaves — diagrammatic: *ax b.*, axillary bud; *gl br*, glandular hair; *hr*, hair; *la d.*, latex duct; *pph*, protophloem; *p v s*, provascular strand; *p x*, protoxylem.

PERICYCLIC FIBERS.—Bredemann (4) and Heuser (15) have pointed out that staminate plants produce fibers of better quality than the carpellate ones; and, despite the fact that the number of carpellate plants slightly exceeds the staminate in a given crop, the percentage of fiber content is greater for the staminate plants than for the carpellate ones.

Early in ontogeny, the pericyclic region becomes multilayered, and the cells which comprise it are noticeably larger than those of the adjacent cortical parenchyma. The pericyclic cells enlarge, elongate, become conspicuously vacuolate, and the cytoplasm finally forms a thin layer against the primary wall. As the process of secondary wall formation continues, the lumen of each fiber becomes increasingly smaller, the cytoplasm is concentrated into a smaller space; and, in some instances, the cell of the nearly mature fiber is wholly filled with a granular cytoplasm. When the fiber is completely mature, the cytoplasm disintegrates so that only traces of desiccated material remain in the elongated oval lumen which occupies about one-third of the transection of the cell.

The wall of the fiber consists chiefly of pure cellulose, but the proportion does not run as high as in the flax fiber. The amount of cellulose in one of the best types of Italian hemp was found to be 77.77 per cent. The cell walls frequently exhibit stratification, resembling those of flax in this respect, but the fibers are less transparent, and the lumen is less easy to distinguish because of surface striations.

In transection, a single fiber is three- to seven-angled; but owing to secondary growth of the stem, it may be much compressed so that the angles become somewhat rounded or flattened. The average diameter is $22\ \mu$; but there is great variation between individual fibers, extremes of 16 to $50\ \mu$ being reported by Matthews (21), and Cross and Bevan (10). The diameter for a given fiber is variable, since the fiber is tapered at both ends, and there is also a wide range in the length, which may vary from 1 to 10 cm. The average is between 3.5 and 4 cm., according to Heuser (15), while Matthews (21) gives a somewhat lower figure, 2 cm. The tips of the fiber cells usually are blunt or rounded, but some are forked, this being regarded as a differentiating characteristic between the northern and southern varieties of hemp, branching being more frequent in the latter. Schilling (27) has pointed out that the bifurcation of hemp fibers can be experimentally induced during

development by a mechanical breaking of the stem over a five- to ten-day period, and that it also occurs in nature due to wind and other mechanical factors. In small healthy plants, he found the fibers free from bifurcation and other abnormal form changes.

THE PREPARATION OF THE FIBER. — In the preparation of the fiber, the plants are harvested, shocked and dried before retting is undertaken. This is accomplished by dew-retting or water-retting, the former being more common in the United States and the latter in Europe and Asia. In dew-retting, the stalks are spread out on the ground and subjected to moisture or to freezing and thawing; while in water-retting, they are placed directly in streams, ponds, or tanks. During this period, bacteria and fungi act upon the middle lamellae of the fibers and on the tissues surrounding them. This is followed by breaking and skutching to remove the disintegrated tissues from the fiber, which is then hackled by hand.

It should be noted that the technical hemp fiber of commerce is not a single fiber cell, but consists of a group of cells which are held together by their middle lamellae. One of the problems of retting to obtain desirable commercial fiber is to insure the dissolution of the middle lamellae which connect the fiber strands with adjacent tissue, and at the same time avoid a complete dissolution of the middle lamellae between adjacent fiber cells.

THE LEAF. — The blade of the leaf is relatively thin and the principal veins form prominent ridges on the abaxial surface while the adaxial surface is depressed into a groove above each vein. (Fig. 116.) The cells of the upper epidermis are considerably larger than those of the lower and much more heavily cutinized. Stomata are infrequent or lacking on the upper epidermis and very numerous in the lower one. Briosi and Tognini (7) made several stomatal counts for the cotyledons, foliage leaves, stipules, and bracts, which are here summarized:

TABLE III

TYPE OF LEAF	NO. OF STOMATA PER SQ. MM.	
	Lower Epidermis	Upper Epidermis
Cotyledons	100	100
Central leaflet	350	13
Foliar bract	700	—
Stipule	53	21
Sepal of staminate flower	100	—
Floral bract	43	24

Epidermal hairs are produced on both surfaces, being more numerous on the lower, and the large persistent hairs produce basal cystoliths. Glandular hairs also occur in large numbers, these being especially noticeable in the young leaf and less so in the mature blade, since they tend to break off with age.

The mesophyll, except adjacent to the principal veins, consists of a single layer of slender, elongated palisade cells which occupy

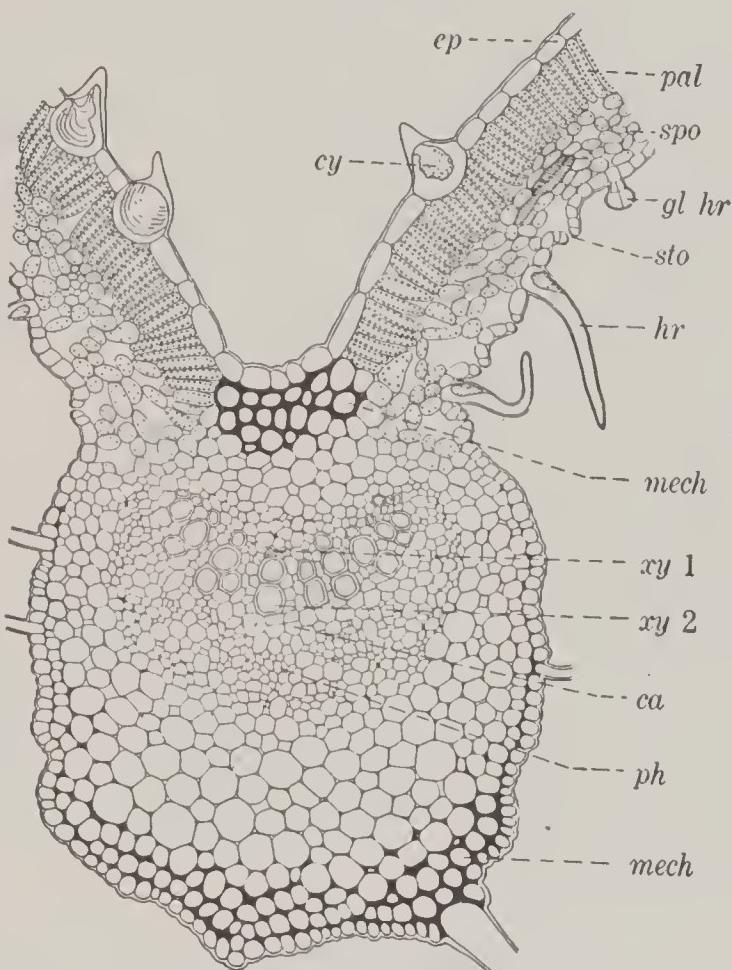


FIG. 116. Transection of a portion of mature leaf through midvein: *ca*, cambium; *cy*, cystolith; *ep*, epidermis; *gl hr*, glandular hair; *hr*, hair; *mech*, mechanical tissue; *pal*, palisade; *ph*, phloem; *spo*, sponge cells; *sto*, stoma; *xy 1*, primary xylem; *xy 2*, secondary xylem. The dark spots in phloem indicate location of latex ducts.

slightly more than half the thickness of the leaf. The spongy parenchyma is very loosely organized, and there are large intercellular spaces leading to the substomatal cavities. The midvein of the leaflet is reinforced by a group of mechanical cells which are located below the groove on the adaxial surface. There is also a zone of mechanical tissue three to four cells in width immediately inside the abaxial epidermis. The vascular bundle is collateral, resembling that described for the stem; and, in the midvein, there

is some development of secondary vascular tissues. Latex ducts occur in the primary phloem and extend into the stem without branching. As in the stem, numerous crystals of calcium oxalate are found in the parenchymatous tissue of the mesophyll and in the phloem parenchyma of the veins.

The petiole is subtriangular in transection with a groove extending along its adaxial surface which is shallow near the base of the petiole and becomes gradually deeper toward the point of divergence of the leaflets. It is strengthened by a zone of collenchyma extending completely around the periphery adjacent to the epidermis, which is somewhat thicker along the abaxial angle and lateral margins. The remaining tissue of the petiole consists of chlorophyll parenchyma, except for the veins. There are three at the base of the petiole, but these usually anastomose in the upper portion of the petiole, forming a continuous crescentic zone from which branches arise that extend into the leaflets.

A situation has been reported regarding the xylem of the petiolar bundles which may be noted here. Alexandrov and Alexandrova (1), in investigating the question as to whether or not lignification of cell walls is an irreversible process, have pointed out that in hemp the oldest xylem vessels in the lower petioles are regularly delignified. According to their account, the walls of the vessels are dissolved completely, even the cellulose, and the vessels are replaced by proliferating parenchymatous cells. In their opinion, this delignification may occur normally to a great extent and is not necessarily connected with pathological or traumatic conditions.

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CHAPTER IX

CHENOPODIACEAE

BETA VULGARIS

THERE are several varieties of *Beta vulgaris* which Bailey (4) has divided into five cultural sections: garden beets, mangels, sugar beets, chard, and foliage beets.¹ The cultivated beet is an herbaceous dicotyledon which normally completes its life cycle in two years; but like its wild ancestor, *Beta maritima* Linn., the biennial habit is variable and under certain conditions the plant may function as an annual or even as a perennial. When growing as a biennial, the beet produces a large, succulent, fleshy tap root with a short crown stem and a rosette of leaves during the first season. In this phase of the vegetative cycle, large food reserves are accumulated in the storage regions of the root which are utilized in the second year; and, after the formation of a second rosette of leaves, the plant develops a bushy shoot and produces its flowering branches. These are stout and angular, and, in some of the seed fields, may attain a height of 5 to 6 feet or more.

GENERAL MORPHOLOGY

THE FLESHY AXIS — Root, Hypocotyl and Stem. — The mature beet of commerce is a pear-shaped or globular fleshy axis made up of a crown, neck, and a more or less elongated tap root. The crown is an unelongated stem from which the rosette of leaves arises, while the smooth hypocotyledonary neck below it, which is devoid of lateral roots, forms the upper portion of the thickened axis. The lower root-like part of the axis is described by Weaver (20) as follows,

"The sugar beet has a strong, deep, very fleshy taproot, which in moist soil grows rapidly and almost vertically downward, reaching

¹ Much of the anatomical work reported in this chapter, especially that of Artschwager, was done in connection with the sugar beet group, but some of the investigations were concerned with table varieties of the Detroit Dark Red type.

depths of 5 to 6 feet. Beginning just below the soil surface and extending to a depth of 6 to 10 inches, laterals occur in two opposite rows on the sides of the roots. These begin to appear when the plants are 6 to 8 weeks old and finally occur in great numbers, 60 to 70 per linear inch. Running horizontally 6 to 18 inches or more on all sides of the plant and branching profusely, they form an excellent absorbing system in the surface foot of soil. Numerous larger and longer branches arise usually at depths of 8 inches to 4 feet. They spread from 6 inches to 2 feet laterally and penetrate deeply into the subsoil. . . . This root habit, however, is greatly modified by variations in soil conditions. In dry soil, the taproot is smaller, pursues a more tortuous course, does not penetrate so deeply, and is branched more nearly to the tip. The larger, deeper seated branches turn downward rather abruptly, reaching depths of 3 to 4 feet. Branching is more profuse throughout. Development of the surface absorbing system may be greatly delayed, although it branches more profusely and may extend even more widely when the soil becomes moist." (Fig. 117.)

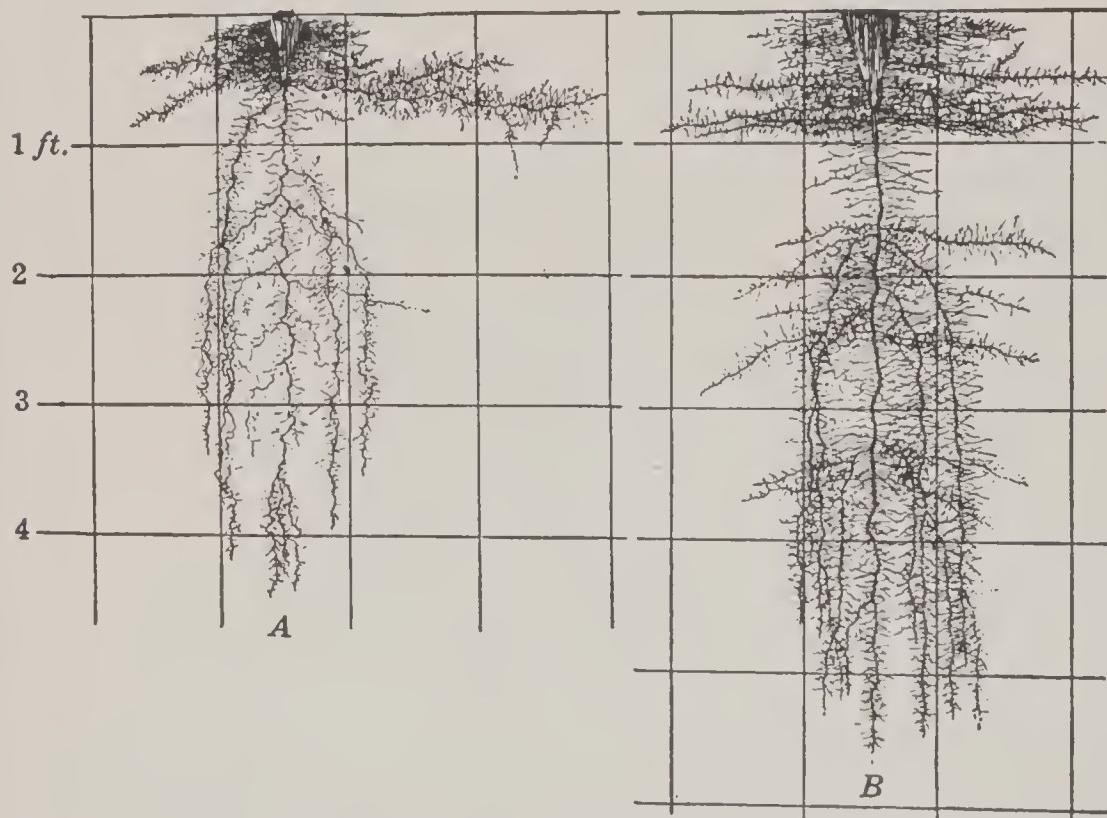


FIG. 117. Diagrams showing habit and extent of root system of the sugar beet grown (A) in dry land; and (B) in fully irrigated soil. (After Weaver, *Root Development of Field Crops*, McGraw-Hill Book Co.)

The two rows of laterals, referred to by Weaver, are usually double rows and the grooves from which they arise are oriented in the same vertical plane as the primary xylem strand of the root. The furrowing and transsectional plan of the fleshy axis can be correlated with the mode of secondary thickening of the axis, and

the manner in which the secondary or lateral roots arise. Typically, the beet has a single tap root, but it may branch to form several fleshy members.

THE LEAVES. — The large succulent leaves of the basal rosette are arranged in a close spiral in a $\frac{5}{13}$ phyllotaxy, and are extremely variable as to size, shape, and color. In general, the petiole is somewhat triangular in transection and more or less flattened at the base. The lamina is prominently veined and the lateral branches which arise from the main veins form a netted system in which some of the small veinlets anastomose, while others end blindly in the mesophyll. The blade is elongated, somewhat oblong or triangular with a cordate base, its margins may be straight or undulate, and the surface is smooth or crinkly. There is an equally wide variation with respect to color, which ranges from dark red to a light green. The rosette of leaves produced the second year resembles that of the first but they are progressively smaller.

THE INFLORESCENCES AND FLOWERS. — The stem elongates rapidly to form the floral axis, and the development of numerous branches which arise from the axillary buds of the basal leaves results in the bushy habit of the mature plant. The terminal portions of the main axes and lateral branches produce inflorescences which are paniculate or spicate in character. (Fig. 118.) The flowers are sessile and occur singly or more commonly in clusters of two or three. They arise from a very short floral branch subtended by a large median bract and two lateral ones which bear flowers in their axils. The flowers are perfect and consist of five narrow sepals, five stamens, and a tricarpellate pistil. The ovary of the mature pistil forms a fruit which is embedded in the base of the perianth of the flower, and these are enclosed by the common receptacle of the flower cluster so that a multiple fruit or "seed ball" is formed by the cohesion of two or three such enclosed fruits. The fruit is hard, containing a single seed and, where flowers occur singly, forms what is known in commercial practice as a "single germ beet seed." When the "seed ball" is formed by the aggregation of two or three flowers, the so-called "multiple beet seed" is produced. These terms, of course, refer to the fruits, as the true seeds are small, dark, kidney-shaped structures.

SEED PRODUCTION. — The annual method of producing sugar beet seed was developed by Overpeck (13) in New Mexico about ten

years ago. The seed is planted about September first, and the plants are allowed to remain unthinned so that they develop tap roots about $\frac{1}{2}$ to $1\frac{1}{2}$ inches in diameter by the time cold weather stops further development. Early in March, the plants begin to produce seed stalks; by the latter part of June, these have reached

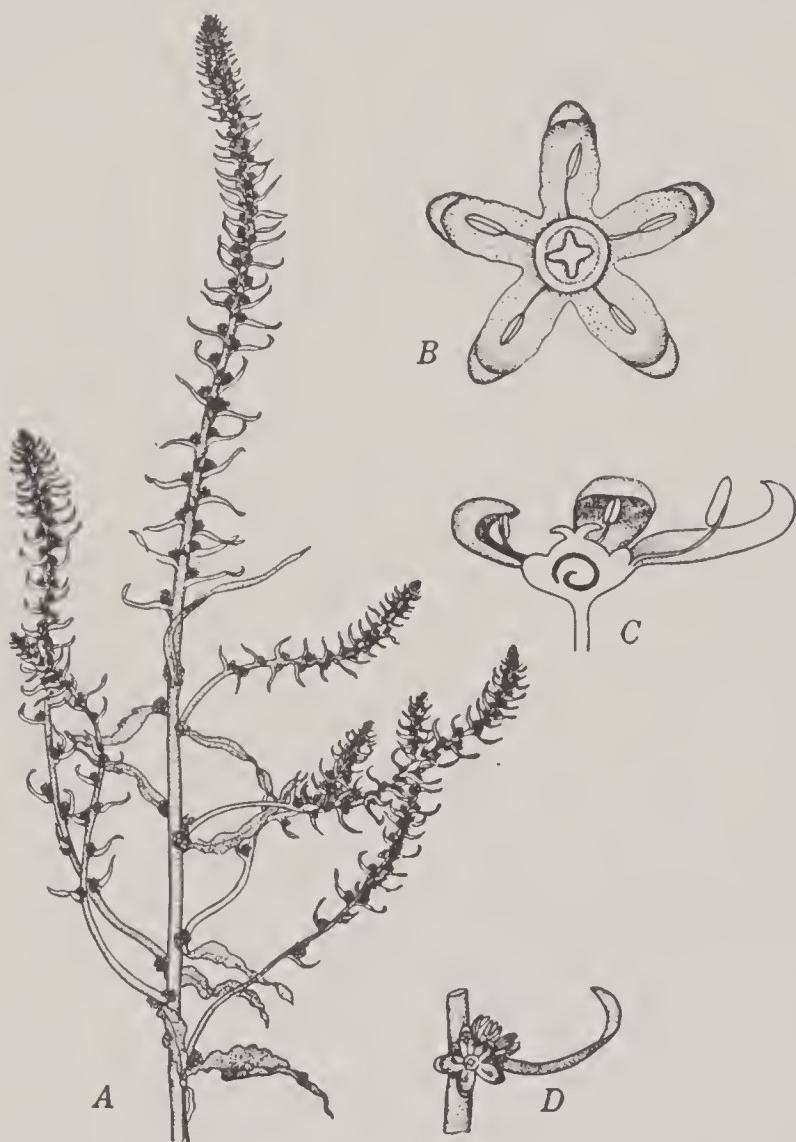


FIG. 118. A, general habit of inflorescences; B, flower, showing arrangement of floral parts; C, longisection through floral axis showing relation of parts; D, single inflorescence showing axillary position of sessile flowers.

a height of from 4 to 8 feet, depending upon soil fertility, and bear clusters of seed-containing fruits. This method requires a climate characterized by winters warm enough to allow the plants to live over without injury, but cold enough to cause the physiological changes which are necessary to throw the plant from the vegetative into the reproductive phase of its cycle. Such conditions exist in southern California, Arizona, New Mexico and southern Utah

and may be easily duplicated in controlled environments in greenhouses.

In Europe, the biennial method is used. It consists in planting the seed in July or August and digging the small beets before frost. The roots are then stored in out-of-door pits over the winter where the low temperatures condition the roots for seed stalk production. In the spring, the roots are replanted, seed stalks develop, and the seed is harvested in July.

THE SEED. — The mature seed is a flat, shiny, reddish-brown structure which ranges from 1.5 to 3 mm. in diameter, and is approximately 1.5 mm. in thickness. The seed coat has two integuments, the curved embryo within completely surrounds the perisperm, and a single layer of endosperm encloses the distal portion of the primary root. (Fig. 119.) Each of the integuments consists initially of two cell layers, except near the chalaza where they are more numerous; but in the mature seed coat, only three remain, since the outermost layer of the inner integument disintegrates during the development of the seed. The cells of the outer integument are at first undifferentiated, but later the outer wall becomes thickened and is covered with an extensive cuticle. The second layer of the outer integument is comprised of small cells with dense contents, and the individual cells are separated from one another by small intercellular spaces. The layers of the inner integument are at first meristematic; but, as maturation of the seed proceeds, the outer layer remains small, the nuclei disintegrate and the cells are obliterated. Meanwhile, the cells of the inner layer of the inner integument enlarge and the walls become delicately sculptured. A thick cuticle is laid down between the inner integument and the nucellus which, according to Bennett and Esau (6), may be recognized by microchemical tests when the embryo consists of approximately nine cells. They point out that the cuticle is lacking in the chalazal region where the phloem approaches the perisperm, so that a "passage region" is formed through which materials can move into the latter. When the seed has reached maturity, the walls of the cells in this zone also become cutinized or suberized, sealing off the embryo and perisperm.

Artschwager (2) reports that "the cells of the outer integument contain starch and there is an extensive tannin deposit in both integumentary layers." The embryo is filled with albuminous

and oily materials and the perisperm is packed with large starch grains except at the chalazal region. Starch is not found in the resting embryo but may appear there during germination. With respect to the movement of reserve foods into the storage tissues of the seed, Bennett and Esau find that the vascular strand which passes through the funiculus is collateral; but after it has entered

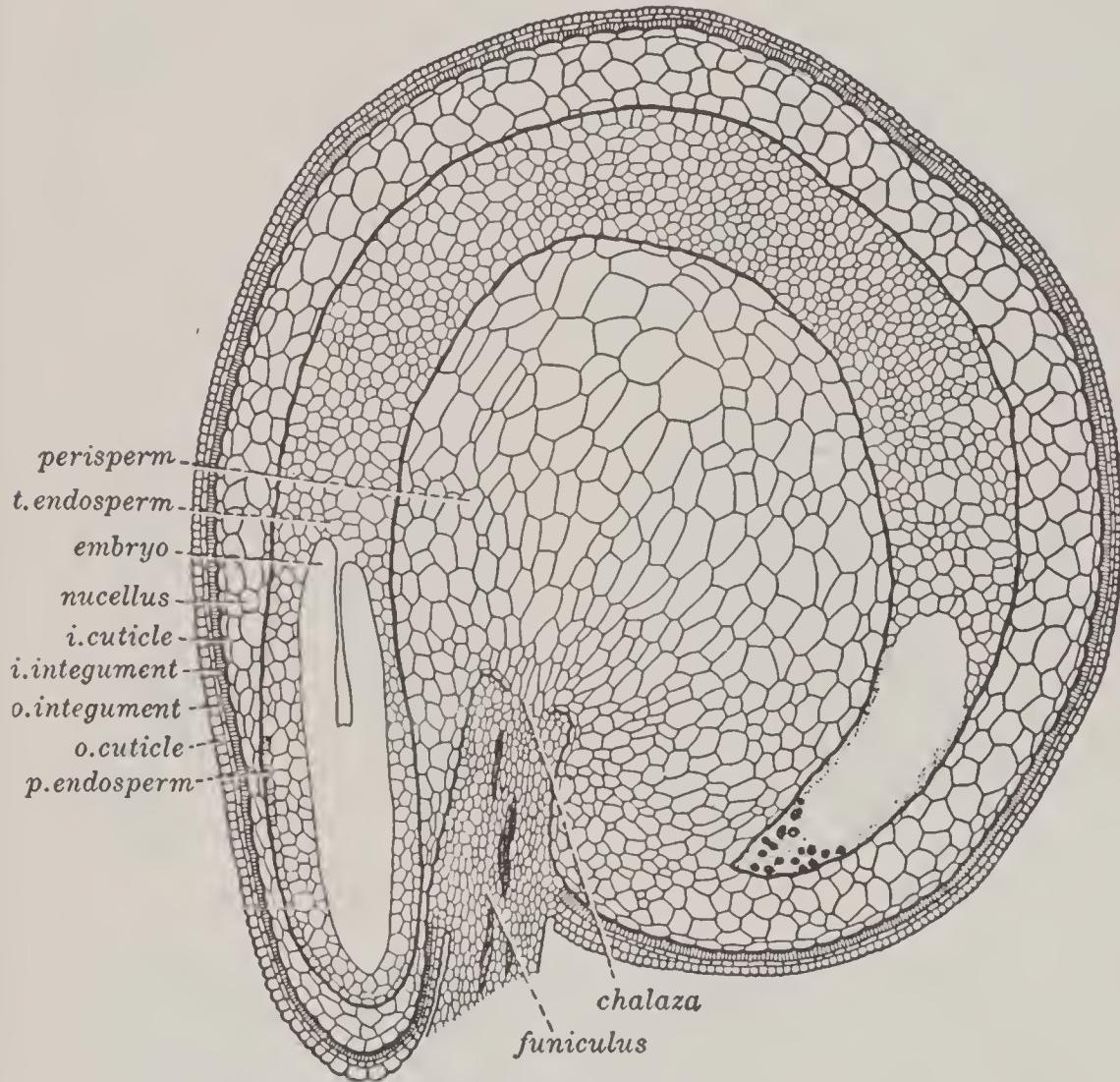


FIG. 119. Section through ovule and young embryo showing structure of seed and seed coat. (After Artschwager, *Jour. Agr. Res.*)

the chalazal region, it tends to be amphicribral, and the phloem extends farther than the xylem. (Fig. 120, A-I.) No direct vascular connection exists between the embryo and the storage tissues adjacent to it, but protoxylem elements are completely differentiated in the cotyledons before germination, and protophloem elements are also present.

DEVELOPMENT OF THE SEEDLING. — Under favorable conditions for germination, the primary root pushes through the seed and

fruit coats of the "seed ball" and grows directly downward without branching. The hypocotyledonary arch elongates, lifting the cotyledons above the soil; and, finally, the hypocotyl straightens

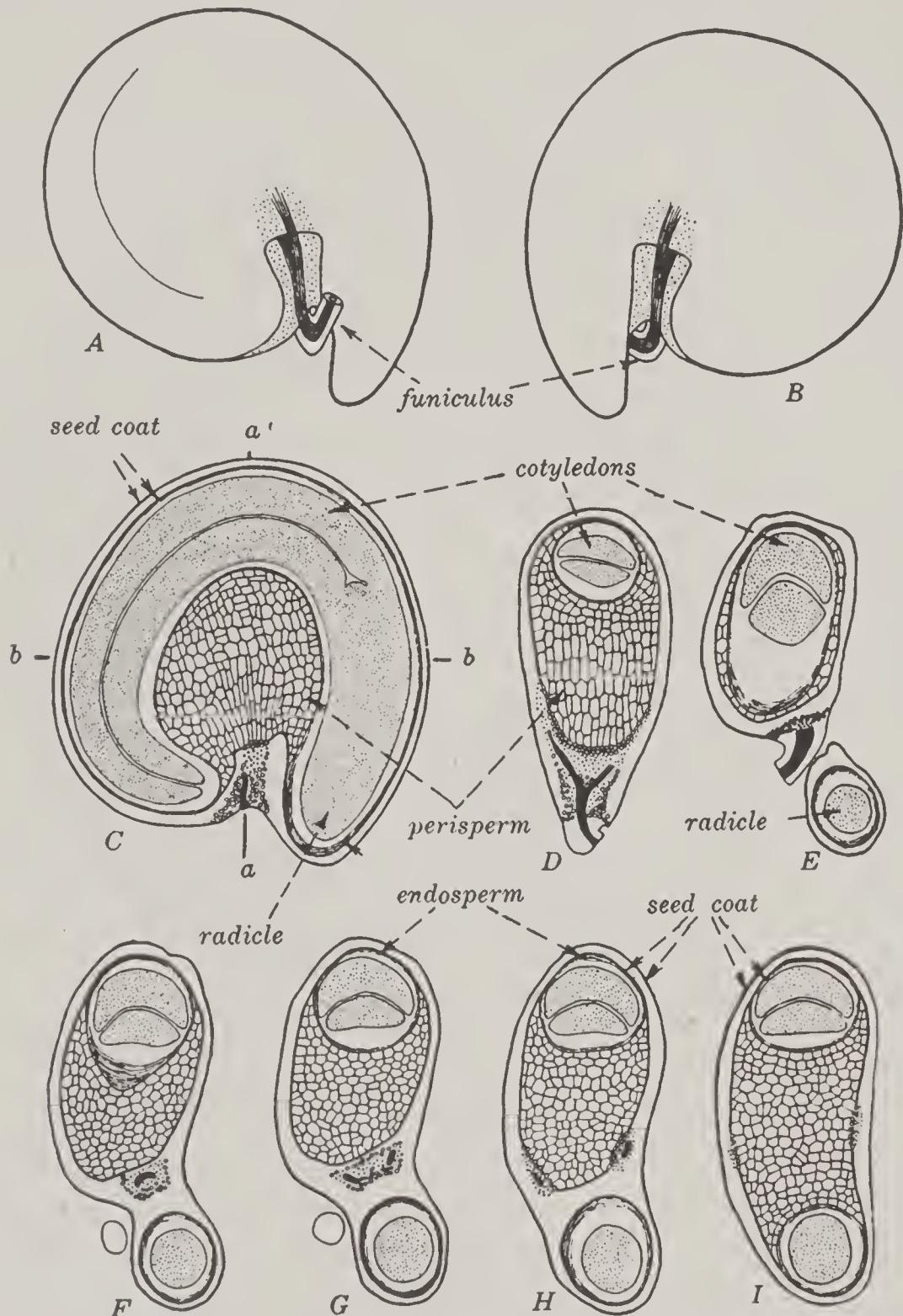


FIG. 120. A-B, diagrams of sugar beet seed showing distribution of vascular tissues; C, section of mature seed with embryo in longisection; D, transection made along axis a-a in C; E-I, successive transections made parallel to axis b-b in C; E is the lowest section. In figures C-I, xylem is shown in solid black, phloem by heavy stippling, and tannin-containing cells by circles. (After Bennett and Esau, *Jour. Agr. Res.*)

and the cotyledons expand laterally. (Fig. 121.) The young seedling consists of three regions, root, hypocotyl, and cotyledons; and the point of transition between root and hypocotyl can be determined with a fair degree of accuracy by the abrupt tapering of the axis and by the location of the lateral roots. Epicotyledonary development is slow; but after the complete expansion of the



FIG. 121. Habit of beet fruit and stages in development of seedling.

cotyledons, the first pair of foliage leaves begins to grow rapidly. This occurs about eight to ten days after germination and is followed by the differentiation and growth of the foliage leaves which form the primary rosette.

ANATOMY

THE COTYLEDONS. — The fleshy cotyledons are single-nerved and elongated with short petioles or tapering bases. Their structure is simple and the mesophyll consists of chlorenchyma in which there is little differentiation into palisade and spongy tissues. The small vascular bundles are collateral and run longitudinally between the spongy parenchyma and the palisade. The epidermal cells are irregularly polygonal in outline with

sinuous walls, and numerous stomata occur with equal frequency in the upper and lower surfaces.

THE PRIMARY ROOT. — The primary root has an exarch, diarch protostele; and, at the time of complete maturation of its primary tissues, consists of an epidermis, cortex, and stele. In the apical region, many of the epidermal cells develop as root hairs; while in the transition zone above the piliferous area, the surface is glabrous and cutinized. The cortical region is comprised of several rows (usually three to seven) of parenchymatous cells with large intercellular spaces, the innermost ones being smaller

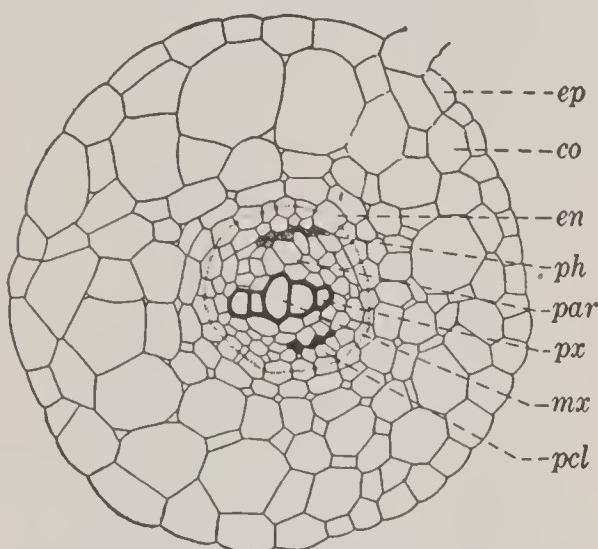
and more regular in shape than those in the peripheral rows. (Fig. 122.) The cortex is limited inwardly by the endodermis, which is single-layered and without intercellular spaces.

The development of Casparyan strips and the later suberization of the walls of the endodermal cells has been investigated by Plaut (15) and Rugeberg (16), whose findings have been confirmed by Artschwager (1). Except for the first few millimeters of the root tip, the endodermal

FIG. 122. Transection of primary root at the maturation of primary tissues: *co*, cortex; *en*, endodermis; *ep*, epidermis; *mx*, metaxylem; *par*, interstitial parenchyma; *pcl*, pericycle; *ph*, phloem; *px*, protoxylem. (Redrawn after Artschwager, *Jour. Agr. Res.*)

cells are characterized by Casparyan strips on the radial and end walls which are detectable with the use of stain techniques at about the time that the metaxylem vessels mature. This secondary phase of the endodermis extends axially for approximately 3 cm., at which level the cells are in the tertiary stage of wall development characterized by the deposition of a suberin layer over the entire surface. This occurs later in the cells lying opposite the protoxylem points than in those in other sectors of the endodermis. In the lower hypocotyl, the endodermal wall-thickenings are in the secondary phase; and, at its upper limits, no well-defined Casparyan strips are laid down.

The development of the root axis and the differentiation of the primary vascular tissues has been investigated by Lyle (11)



and Artschwager (1). Their results are here summarized and quoted in part. The ontogeny follows Janczewski's (10) third type, in which the plerome and periblem give rise to the stele and cortex respectively, while the surrounding calyptrogen-dermatogen layer initiates the epidermis and the root cap. According to Lyle (11),

"this calyptrogen-dermatogen layer of cells, overlying the periblem, divides periclinally adding a layer of cells to the root cap and renewing the initial layer itself. The marginal cells of this new calyptrogen-dermatogen layer farthest from the root apex divide only anticlinally forming epidermal cells. This distal portion of the dual layer is thus a dermatogen while the remaining apical section is the calyptrogen. This method of formation of root cap and epidermis accounts for the stair-step arrangement of the latter. (Fig. 123.) Cells of the layers of the root cap also divide anticlinally thus compensating for the increase in length of the underlying zones of the root axis. Segments of a few rows of the root cap may also divide periclinally forming additional short layers in the root cap.

"The cortex is derived from the periblem, which consists of a single layer of cells directly inside the calyptrogen-dermatogen. These cells divide both periclinally and anticlinally resulting in three to seven rows of typical cortical cells and an inner layer of axially elongated cells, the endodermis.

"The stele is differentiated from a group of plerome cells that divide in all planes. The outer layer forms the pericycle which is composed

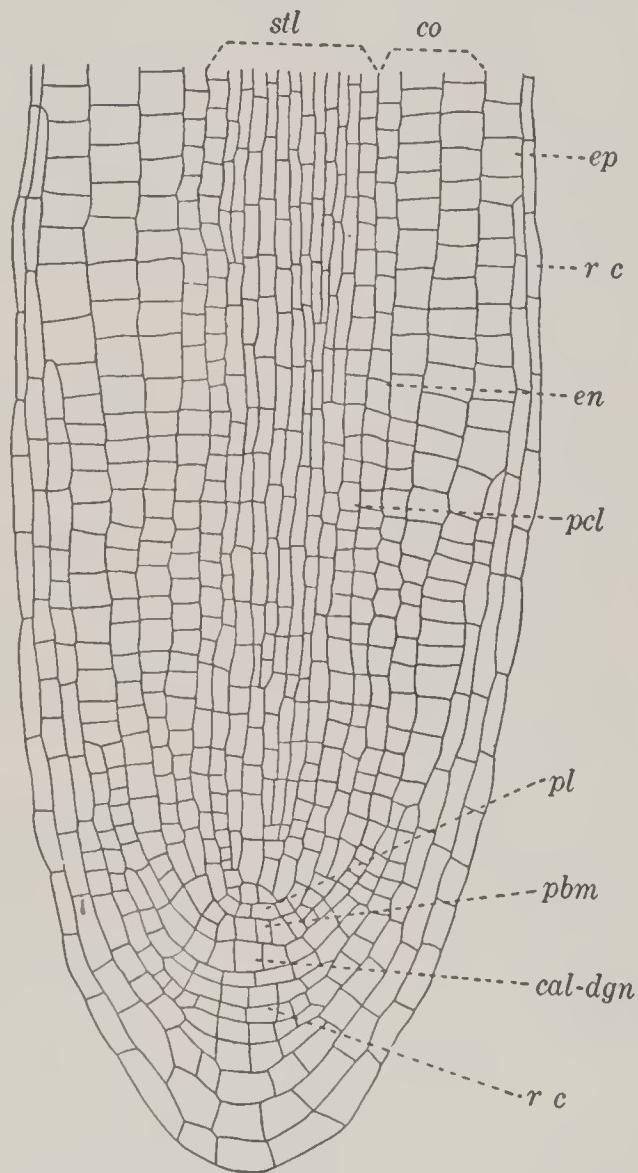


FIG. 123. Longisection of root tip showing histogens: *cal-dgn*, calyptrogen-dermatogen; *co*, cortex; *en*, endodermis; *ep*, epidermis; *pbm*, periblem; *pcl*, pericycle; *pl*, plerome; *rc*, root cap; *stl*, stele. (After Lyle.)

of cells that are more or less rectangular in longitudinal section. About two millimeters above the plerome initials, the primary tissues of the stele begin to differentiate from the elongated procambial cells. Seeliger (17) found the first differentiation to occur in two cells adjacent to the pericycle and 180° from each other. These are the initials of the two groups of primary phloem cells. Protoxylem elements are later differentiated in a plane at right angles to these phloem groups. Differentiation begins in the cells bordering the pericycle and progresses toward the center of the axis. The three or four outermost protoxylem elements have annular or spiral thickenings. The metaxylem vessels in the center of the plate are larger in diameter and have reticulate or scalariform thickenings. As soon as the plate is completely differentiated, cells on the lateral faces of the same mature as metaxylem vessels or parenchyma."

Artschwager's account of the primary xylem formation is essentially like that of Lyle, but he regards the protoxylem as being continuous across the entire primary xylem strand and the metaxylem as being lateral to this continuous zone:

"Differentiation in the protoxylem progresses centripetally until the two protoxylem points meet in the center to form the primary xylem plates. From now on xylem cells mature to the right and left of the xylem plate until all the cells of the primary wood have been formed."

Further differentiation of the primary phloem is not easy to describe because of the small size of the elements, but Seeliger (17) has reported that the metaphloem differentiates from the procambium one or more cells to the inside of the pericycle and that it consists of sieve tubes, companion cells, and phloem parenchyma.

THE VASCULAR TRANSITION. — As Artschwager has pointed out, "the change from the exarch condition in the root to the endarch condition in the upper hypocotyl is very abrupt, with the transition region extending over only a few millimeters"; but complete transition of the primary vascular elements to the collateral endarch arrangement is only attained in the blade of the cotyledon. Lyle (11) described and figured the transition in the Detroit Dark Red variety which occurs chiefly in the region that later forms the fleshy portion of the axis:

"The lower portion of the hypocotyl is root-like in the arrangement of the vascular tissues, resembling the primary root previously described in this respect. (Fig. 125, A.) The first indication of a change in the vascular arrangement occurs in the upper third of the hypocotyl where there is a gradual reorientation of the primary vascular tissues

at successively higher levels until the endarch condition is attained in the blade of the cotyledon. Since the tissues of the hypocotyl differentiate at varying rates; maturing progressively towards the cotyledonary plate, the lower portion in a young seedling may show

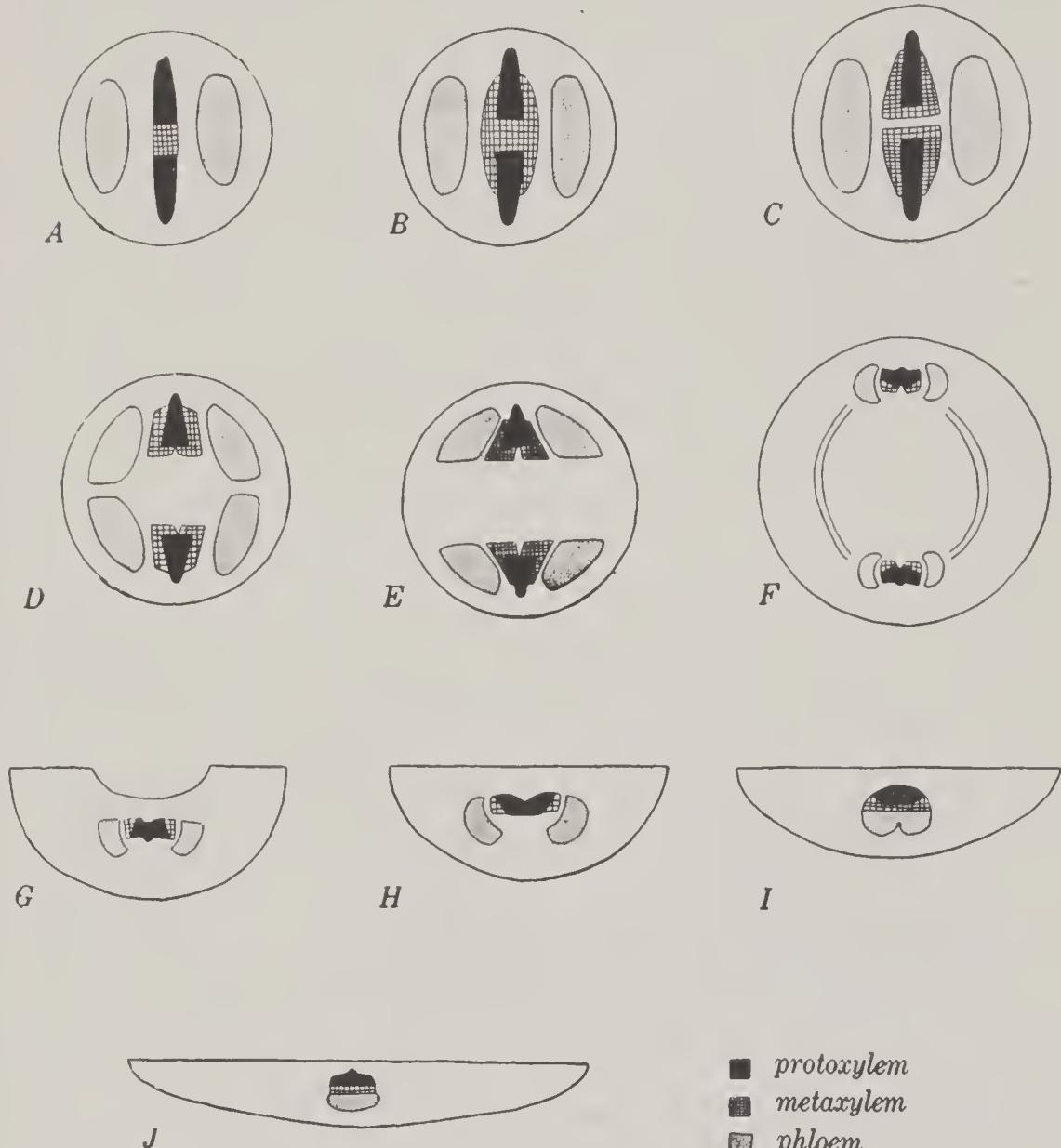


FIG. 124. Diagrams showing vascular transition: *A*, root with diarch xylem strand of proto- and metaxylem; *B*, lower hypocotyl, lateral differentiation of metaxylem; *C*, two-thirds distance between root and epicotyl, reorientation of xylem, circumferential extension of phloem; *D-E*, upper third of hypocotyl, primary xylem separated into two groups by parenchyma, lateral orientation of metaxylem; *F*, cotyledonary node; *G-H*, cotyledonary petiole; *I*, base of cotyledonary blade, adaxial differentiation of protoxylem and abaxial development of metaxylem; *J*, blade with endarch primary xylem. (After Lyle.)

primary tissues completely differentiated and the beginning of secondary thickening while in the upper part the primary tissues are just beginning to mature. The meristematic condition of the region near the cotyledonary plate accounts for the continued elongation of the upper hypocotyl.

- "As indicated in Figure 124, C, and Figure 125, B, the primary xylem plate is separated into two distinct units by parenchyma. These parenchymatous cells are thin-walled, rectangular in longitudinal section, and polygonal or nearly round in cross section. The radially

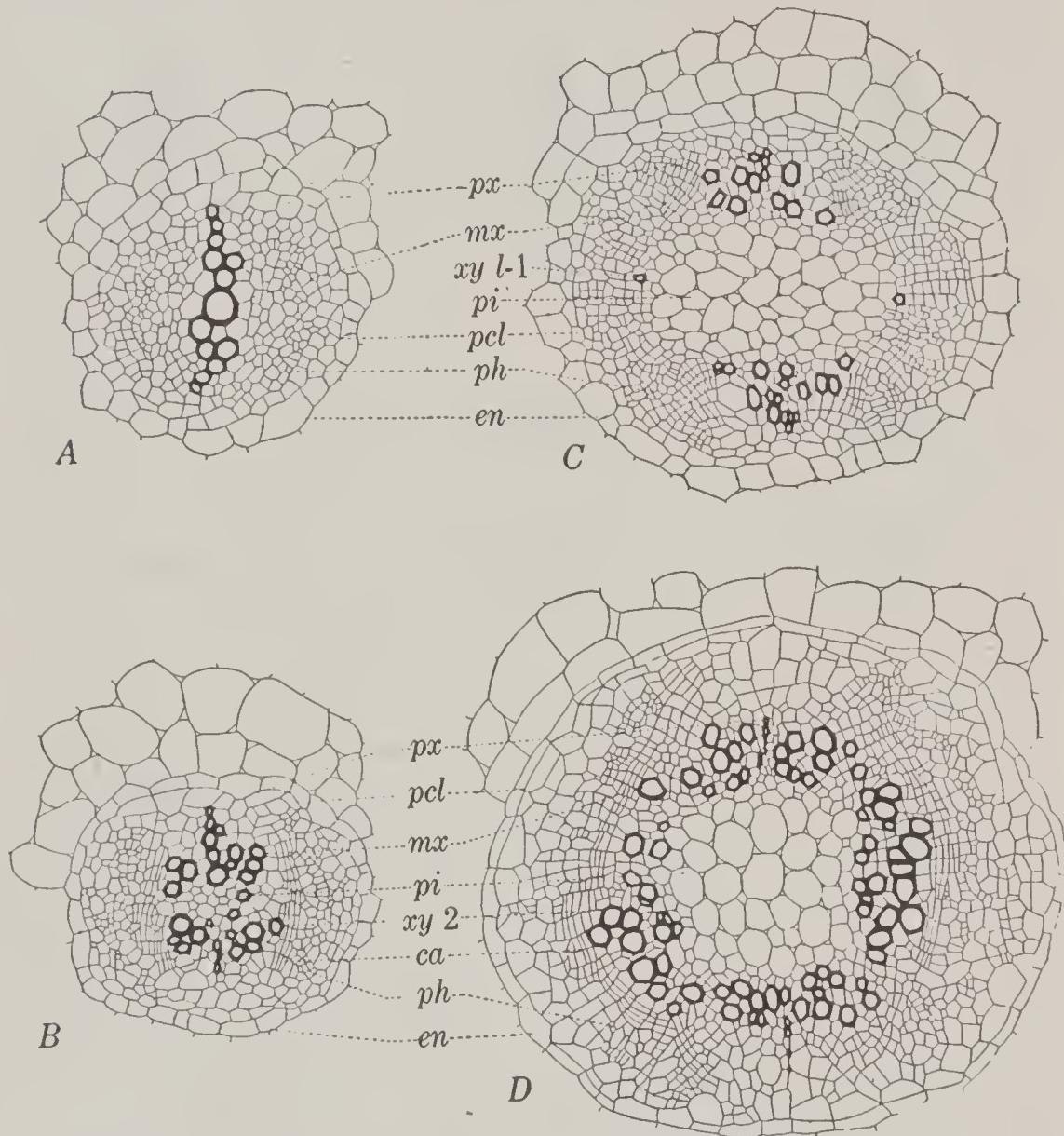


FIG. 125. A, transection of lower hypocotyl, diarch primary xylem strand; B, transection of upper hypocotyl about two-thirds distance between root and epicotyl; C, transection at slightly higher level in hypocotyl; large pith; lateral differentiation of metaxylem; xylem of bundles of first and second foliage leaves; D, transection of cotyledonary plate region; continuous cylinder of vascular tissue composed of cotyledonary bundles and leaf bundles: *ca*, cambium; *en*, endodermis; *mx*, metaxylem; *pcl*, pericycle; *ph*, phloem; *pi*, pith; *px*, protoxylem; *xy 2*, secondary xylem; *xy l-1*, xylem of first foliage leaf. (After Lyle.)

arranged phloem groups on either side of the xylem plate have enlarged circumferentially.

"The diameter of the stele becomes greater at successively higher levels due to an increase in the number of parenchymatous cells at the center of the axis. The units of primary xylem appear to be farther

apart although the protoxylem points are approximately in the same position with reference to the diameter of the axis. The metaxylem vessels occupy a more and more lateral position with respect to the protoxylem, and the phloem masses show a slight division into two units, being separated from each other by cells of the fundamental parenchyma. (Fig. 124, D.)

"The metaxylem continues to differentiate more and more tangentially with reference to the protoxylem in the upper hypocotyl. With the protoxylem point as the common apex, it forms two sub-triangular groups which occupy a collateral position with respect to the phloem groups. (Fig. 124, E and Fig. 125, C.) The vascular system of the hypocotyl in the region of the cotyledonary plate is a dissected siphonostele made up of two cotyledonary bundles and the bundles of the foliage leaves. (Fig. 126, A.) The cotyledonary traces diverge from the stele quite abruptly. In the cotyledonary bundle the primary xylem is still approximately exarch, but the metaxylem vessels have differentiated more laterally forming the vascular strands which Thomas (18) designates as 'double bundles.' (Fig. 124, F and Fig. 127, B.)

"At increasing distances from the cotyledonary node, in the cotyledonary petiole and blade, the protoxylem occupies a more and more adaxial position and the metaxylem a more abaxial one. (Fig. 124, G, H, I, and Fig. 127, C, D.) Thus, the endarch condition of the primary xylem is finally attained in the blade of the cotyledon. (Fig. 124, J.) The phloem groups in the 'double bundles' are separated from each other by parenchyma, but at the level at which the primary xylem is endarch they differentiate as one group in an abaxial position to the metaxylem."

THE EPICOTYL. — The first two foliage leaves develop from the growing point of the unelongated epicotyledonary axis which is surrounded by the bases of the cotyledons. The provascular strands develop early in the leaf primordia, and all the primary bundles of the leaf and epicotyledonary axis are collateral and endarch. The trace of the first foliage leaf above the cotyledons consists of a large central bundle and two smaller lateral ones which pass into the cortex independently, but the laterals anastomose with a vascular strand which continues into the internode above. From (8) has designated this combined strand as a "cauline" bundle. The leaf trace is differentiated downward into the nodal region of the cotyledon where the two "cauline bundles" and the central bundle of the trace anastomose. This endarch bundle gradually becomes smaller in the upper hypocotyl and finally ends blindly in the fundamental parenchyma between the cotyledonary bundles. (Fig. 125, C.) The maturation of the

primary tissues is accompanied by the formation of fascicular and interfascicular cambiums which produce a continuous cylinder of secondary tissues, and these form the only connection

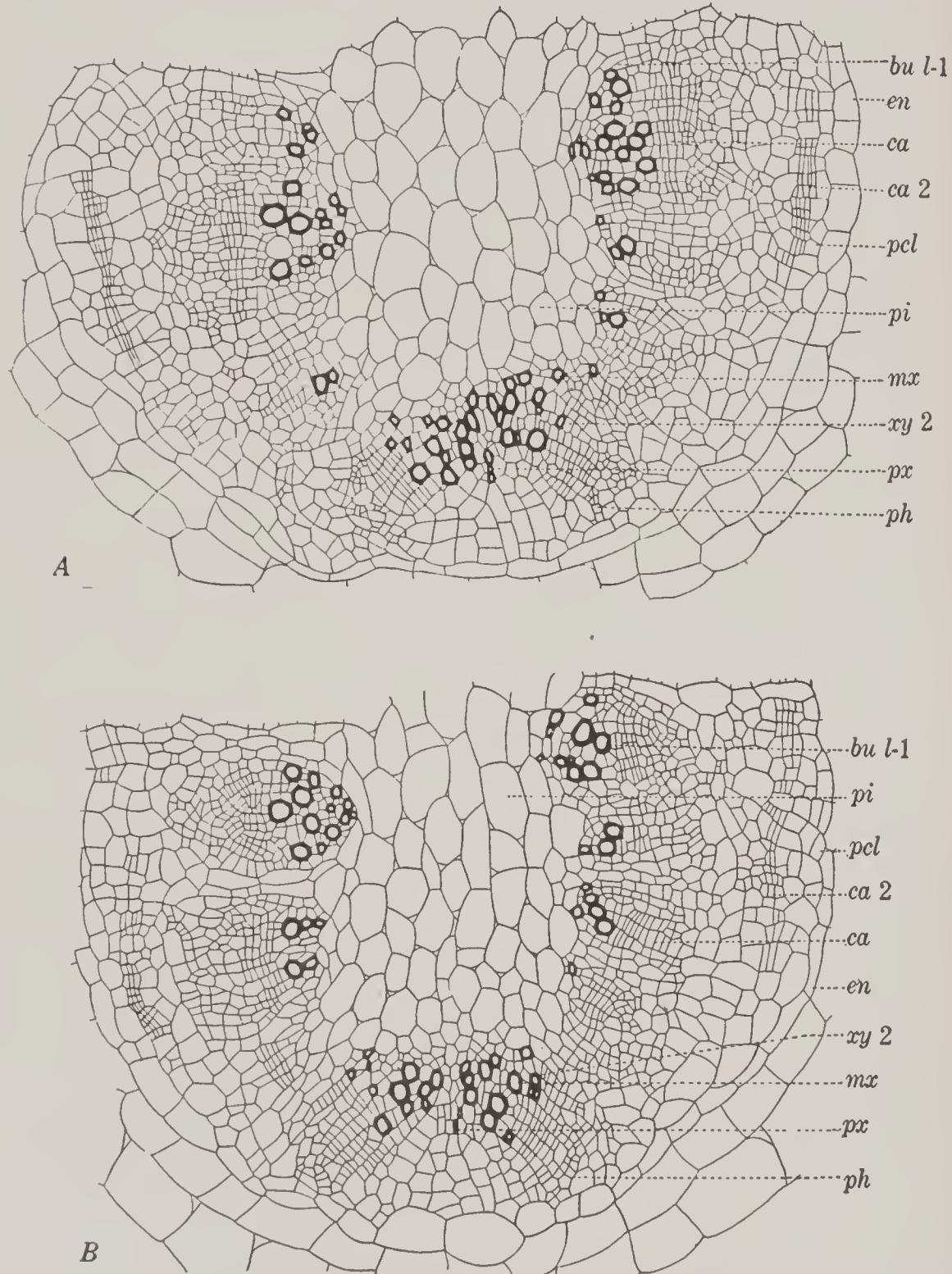


FIG. 126. *A*, transection of portion of upper hypocotyl of older seedling showing cotyledony bundle and those of first and second foliage leaves; *B*, same axis at slightly higher level showing further differentiation of leaf bundles: *bu l-1*, bundle of first foliage leaf; *ca*, cambium; *ca 2*, secondary cambium; *en*, endodermis; *mx*, metaxylem; *pcl*, pericycle; *ph*, phloem; *pi*, pith; *px*, protoxylem; *xy 2*, secondary xylem. (After Lyle.)

between the vascular systems of the hypocotyl and epicotyl. (Fig. 125, D.)

THE ONTOGENY OF THE FLESHY AXIS. — The enlarged fleshy portion of the axis is chiefly root-like, but the upper limits of the hypocotyl are transitional with respect to the arrangement of the primary vascular tissues. In the center of the fleshy portion of the root, there is a small star-shaped region of vascular tissue which consists of the elements of the primary xylem strand and

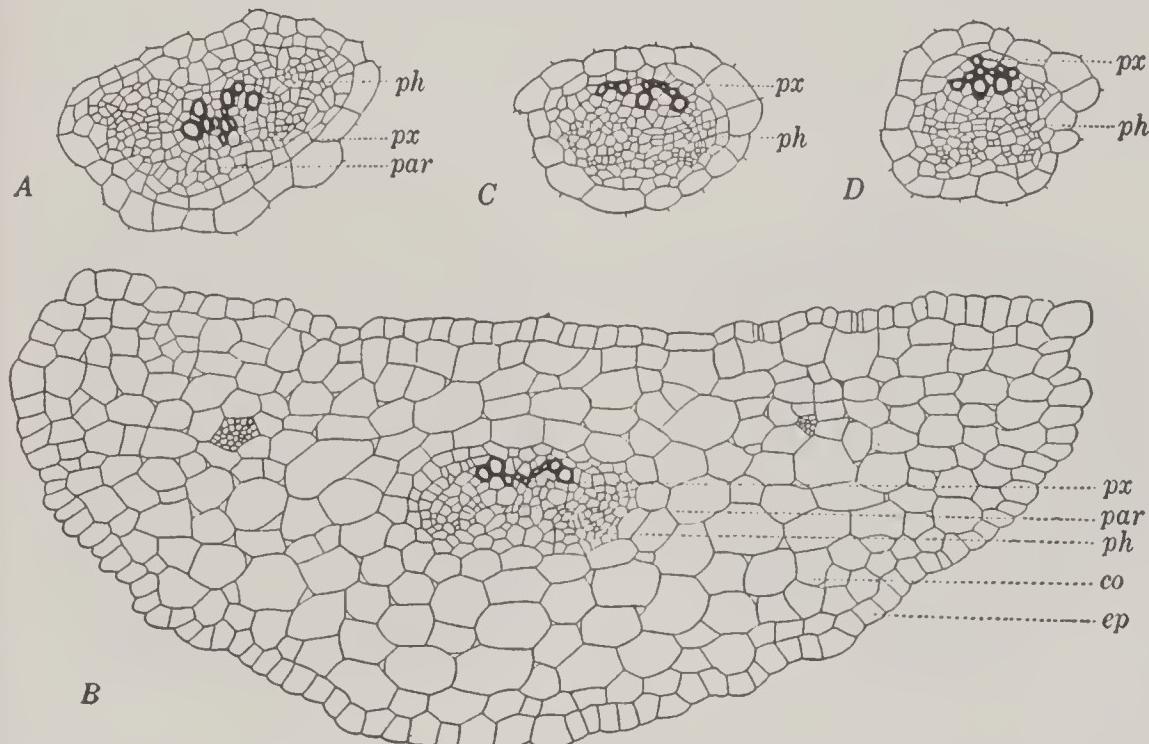


FIG. 127. *A*, cellular drawing of cotyledonary bundle, below level of *B*, the primary xylem still approximately exarch; *B*, transverse section of cotyledon showing protoxylem in a more adaxial position and metaxylem more abaxial than in *A*. The two phloem groups are still separated from each other by parenchyma; *C*, bundle of cotyledon showing further reorientation of protoxylem and metaxylem; *D*, bundle of cotyledon showing endarch primary xylem; the phloem groups have differentiated in a single unit abaxial to the xylem: *co*, cortex; *ep*, epidermis; *par*, parenchyma; *ph*, phloem; *px*, protoxylem. (After Lyle.)

the secondary xylem formed from the primary cambium. Outside this central region is a series of concentric rings of vascular tissue which alternate with bands of storage parenchyma. The number of vascular rings may vary from four to ten or twelve or more, but only four or five of the inner rings contain many mature vascular elements, the outermost ones being very narrow and remaining in a more or less meristematic condition. (Fig. 128.)

A reduction in the number of rings occurs toward the hypocotylary portion of the axis adjacent to the crown stem; and, at this point, many anastomoses of vascular elements occur in connection

with the insertion of the bundles of the leaf traces. There may also be a reduction in the number of rings in the narrow tapering portion of the lower root. Chiefly because of differences in cultural conditions, there is considerable variation in the development of the beet with respect to the number of rings, their width, and the amount of parenchymatous storage tissue, but the fundamental organization of the fleshy axis is identical in all cases.

At the time when the primary tissues are completely matured, the root has a single-layered epidermis, a cortical region consisting of a few layers of parenchyma limited centripetally by the



FIG. 128. Transection of fleshy portion of the axis showing central zone of primary and secondary vascular tissues and concentric rings of tertiary tissues produced by the secondary cambiums. (After Artschwager, *Jour. Agr. Res.*)

endodermis, and the stele. The stele is bounded by a uniseriate pericycle enclosing the primary xylem and phloem, and these are separated from each other by a zone of interstitial parenchyma which increases in amount during the maturation of the primary vascular tissues. This takes about 10 to 12 days and is complete when the axis is only 1 or 2 mm. in diameter in contrast to a final one of 15 cm. or more which may be attained in the mature sugar beet.

When the primary tissues are nearly mature, the first lateral roots originate in the pericycle approximately outside the protoxylem points. They occur in two double longitudinal rows, since the root primordia are initiated slightly to the right and left of radii passing through the two protoxylem points. The

lateral roots are slender and differ from the fleshy, primary root chiefly in having a larger proportion of xylem elements, especially vessels, and in the absence of any considerable amount of ray parenchyma cells. Artschwager (1) has also observed in this connection that the primary xylem strand of the lateral roots is occasionally "triarch instead of diarch, which is always the case in the taproot."

SECONDARY THICKENING. — The great increase in the size of the axis is due to the activity of primary and secondary cambiums. The cells of the interstitial parenchyma begin to elongate axially and divide tangentially, forming the primary cambium which cuts off secondary vascular elements that are centripetally placed in relation to the primary phloem groups and abut the metaxylem. (Fig. 129.) In some instances, there may be a layer of interstitial parenchyma remaining between the primary xylem and the first-formed secondary xylem. The production of secondary xylem and phloem proceeds simultaneously and there is also a progressive lateral extension of the two initial regions of cambial activity toward the protoxylem points, so that finally the primary cambium forms a complete cylinder involving sectors of the pericycle outside the protoxylem. The cambium in these sectors does not produce vascular elements, but cuts off successive layers of parenchymatous cells so that two wedge-shaped xylem rays are formed. These rays may be regarded as pericyclic in cases where the production of the ray parenchyma is the result of a general division of the pericyclic cells, compensating for the growth of the adjacent tissue, rather than the product of a definite cambial layer that cuts off parenchymatous cells reciprocally.

The development of the secondary tissues of the stele results in modifications of the primary tissues lying outside this region.

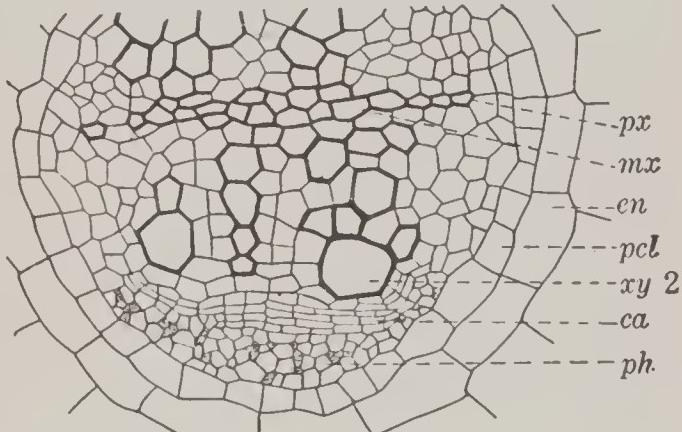


FIG. 129. A portion of stele of primary root in transection showing early stages in secondary thickening: *ca*, cambium; *en*, endodermis; *mx*, metaxylem; *pcl*, pericycle; *ph*, phloem; *px*, protoxylem; *xy 2*, secondary xylem.

The primary phloem keeps pace with the stelar growth by continued divisions of the parenchyma, and the effect of this is to scatter and stretch the sieve tubes until they are finally obliterated. The pericycle also persists, undergoing continued radial divisions of its cells; and, by the time the epidermis and cortical regions are ruptured, it is several-layered as a result of successive periclinal divisions. In the outermost of these layers, periderm formation is initiated at about the time that the first secondary cambiums are beginning to form, this coinciding roughly with cortical disintegration. The phellogen cuts off phellem or cork cells centrifugally and phellodermal cells centripetally, but the divisions do not take place in regular alternation and more cork cells are cut off than phellodermal cells. The outer cork cells are shed continuously as the axis enlarges so that the phellem maintains a relatively constant thickness of from five to eight cell layers. The cork cells are flattened and the thin walls are suberized except for the lignified middle lamella.

THE SECONDARY CAMBIUM. — The first of the rings¹ of the fleshy axis is formed by the activity of the primary cambium. The remaining rings are produced by supernumerary or secondary cambiums, the first of which arises while the formation of the first ring by the primary cambium is still in progress.

TERTIARY THICKENING. — The origin of the supernumerary cambiums and the mechanism of secondary and tertiary thickening has been described by van Tieghem (19), de Bary (5), and Art-schwager (1). According to the latter, the point of origin of these cambiums varies with the level of the axis concerned. In the root and lower hypocotyl, the first supernumerary cambium originates in a zone of primary phloem parenchyma between the pericycle and the secondary phloem. (Fig. 130.) In the upper hypocotyl, it arises from the pericycle; and in the intermediate region, from either the pericycle or phloem parenchyma. Outside the protoxylem points, all secondary cambiums are of pericyclic origin. The formation of additional cambiums then takes place in the following manner:

¹ The use of the term *ring* in the description of the secondary and tertiary thickening of the fleshy axis in this and succeeding sections is one of convenience and applies to the trans-sectional aspect of the axis. Actually, each ring should be regarded as a conical layer of tissue; and the secondary and tertiary rings of the axis as consisting of a series of successively larger cones each of which encloses the one centrad to it.

"When the cambium initial undergoes the first division, the outer of the two daughter cells becomes the initial of a new supernumerary cambium while the inner daughter cell divides further and produces xylem, phloem and medullary ray tissue. This process is repeated until all supernumerary cambiums have been formed. However, there is no uniform method governing the formation of the supernumerary cambiums. Often sections of two supernumerary cambiums originate simultaneously, one from an inner, the other from a more peripheral phloem parenchyma cell. Since most of the supernumerary cambiums of the beet are initiated in quick succession, a beet no thicker than a pencil contains practically all annular zones of growth developing simultaneously."

An alternative explanation of the mechanism of tertiary thickening accounts for the origin of the secondary cambiums as a result of the continued activity of the pericycle. Early in ontogeny, the pericycle becomes an actively dividing multi-layered zone which keeps pace with the enlargement of the axis. It seems probable that the secondary cambiums arise in fairly rapid succession from the pericyclic parenchyma; but there may be some time elapsing between the formation of the successive cambiums. During this interval, those already formed function actively in producing the tissues of their respective rings while the remaining pericyclic tissue is increased by continued radial and tangential divisions. This would harmonize with the fact that the innermost rings are the widest ones. (Fig. 128.) In either case, the pericycle perpetuates itself as the outer zone of the axis and produces a phellogen which forms cork and phellodermal cells.

Regardless of what explanation is advanced for the mode and sequence of origin of the secondary cambiums, there is

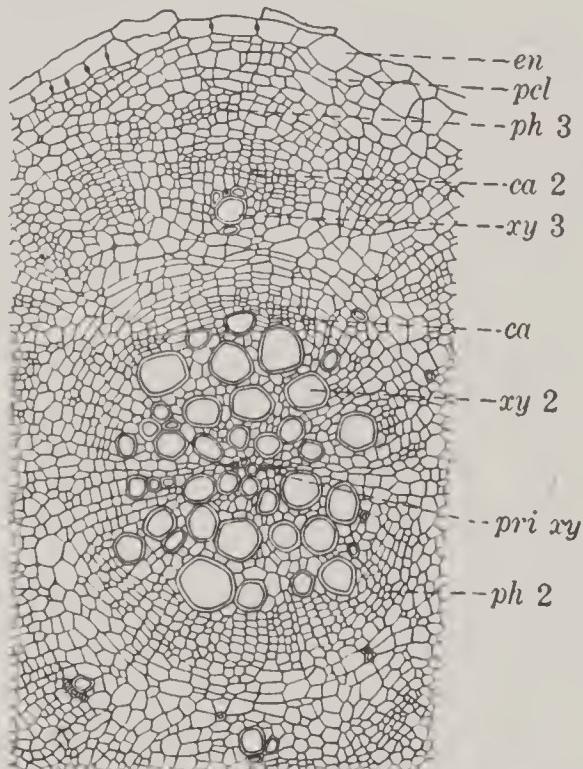


FIG. 130. Transection of portion of stele of primary root showing primary xylem, secondary thickening and initiation of tertiary thickening: *ca*, primary cambium; *ca* 2, secondary cambium; *en*, endodermis; *pcl*, pericycle; *ph* 2, secondary phloem; *ph* 3, tertiary phloem; *pri xy*, primary xylem; *xy* 2, secondary xylem; *xy* 3, tertiary xylem.

a general agreement as to the subsequent development of tissues derived from them. There are commonly five or six relatively wide

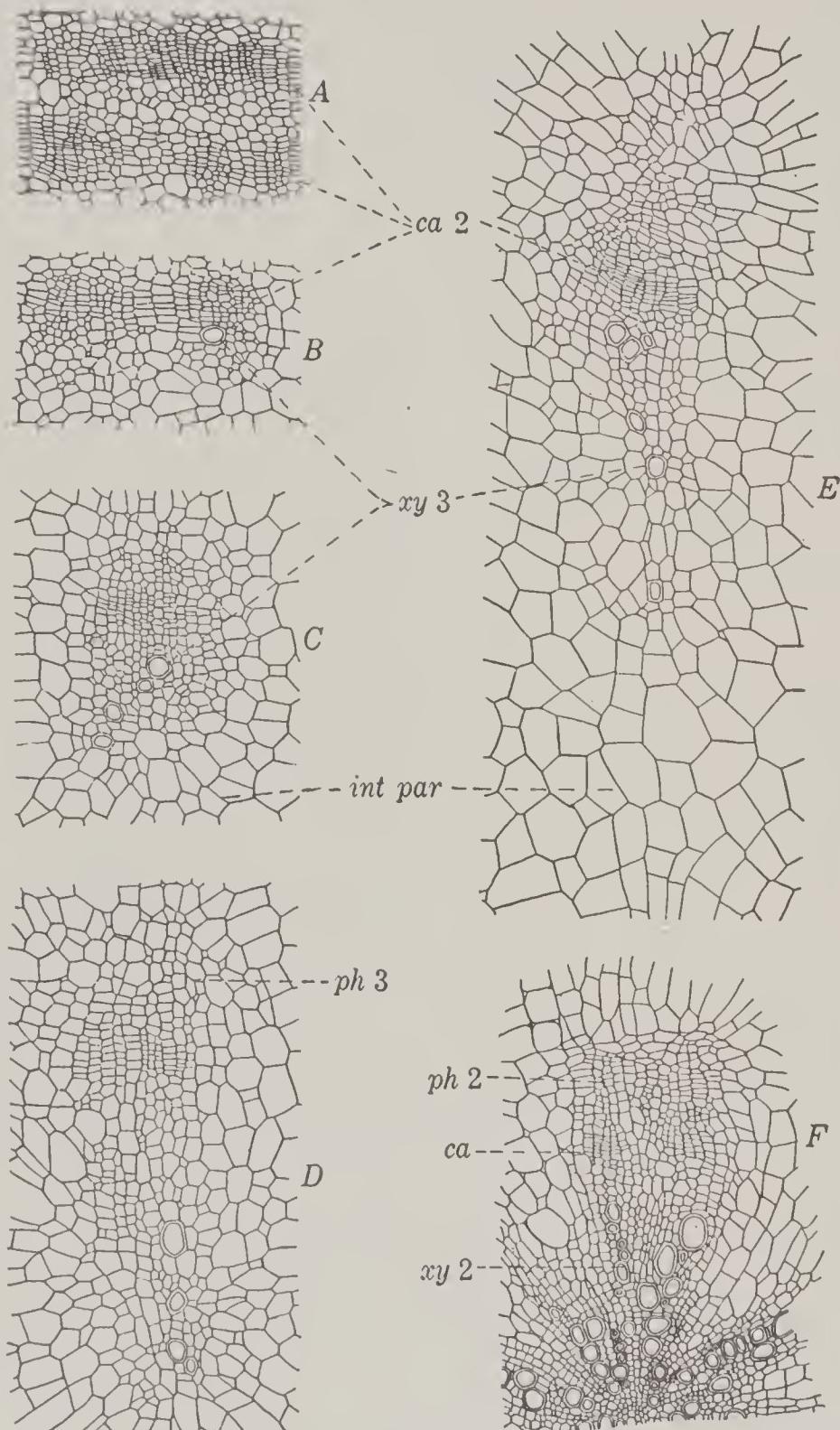


FIG. 131. *A-E*, sectors of successive secondary cambiums from peripheral one, *A*, to one of innermost rings, *E*, showing progressive development of rings; *F*, sector of central portion of stele showing primary cambium and secondary tissues derived from it: *ca*, primary cambium; *ca 2*, secondary cambium; *int par*, interzonal parenchyma; *ph 2*, secondary phloem; *ph 3*, tertiary phloem; *xy 2*, secondary xylem; *xy 3*, tertiary xylem.

concentric rings, outside of which there may be several narrower ones; but the inner rings are not equal in width, each being narrower than the one centrad to it. This indicates that, in ring formation, the activation of the successively formed secondary cambiums is centrifugally progressive; and that several of them are functional at one time. (Fig. 131.)

Because of this mode of development, it is possible to determine the ontogeny of one ring by studying successive rings in a centripetal direction. The outermost one, lying immediately within the periderm, is entirely meristematic, consisting of cambial cells derived from the pericycle, parenchyma, and undifferentiated vascular elements. The first of these to differentiate are sieve tubes and companion cells which may generally be found in the second youngest ring. (Fig. 132, B.) Following this, there is a differentiation of a large number of phloem parenchyma cells which by their later divisions and enlargement separate the sieve tubes and companion cells from the cambium ring that produced them. Ultimately, these first-formed phloem elements are obliterated and crushed. (Fig. 132, F.) In most cases, the xylem elements are arranged in narrow radial bands and are separated from each other tangentially by zones of ray parenchyma. (Fig. 133.) In general, the production of phloem cells precedes the differentiation of xylem cells in any given ring; but, occasionally, the production of vascular elements is reciprocal.

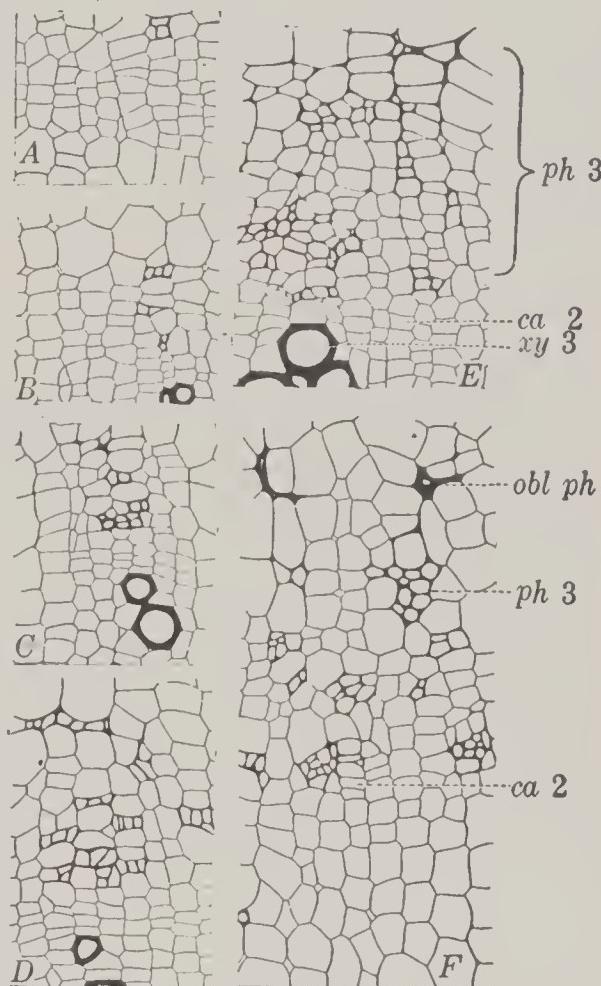


FIG. 132. Ontogeny of phloem: A, most peripheral ring; B, second ring; C, third ring; D, fourth ring; E, fifth ring; F, fifth ring but from a different part of the beet. The phloem shows a very marked degree of development compared with the xylem. The outermost phloem groups in F are already obliterated: ca 2, secondary cambium; obl ph, obliterated phloem; ph 3, tertiary phloem; xy 3, tertiary xylem. (After Artschwager, *Jour. Agr. Res.*)

The manner in which the vascular elements are distributed indicates that the secondary cambiums do not occur as complete rings, but consist of discrete sectors derived from the pericycle. The parenchymatous cells which intervene between the radial rows of vascular elements are of pericyclic origin and may be regarded as pericyclic rays. Each cambium produces a zone of parenchymatous cells centripetally before the tertiary xylem elements are differentiated; and further growth and division of these cells results in a radial or, occasionally, a tangential displacement of the xylem elements.

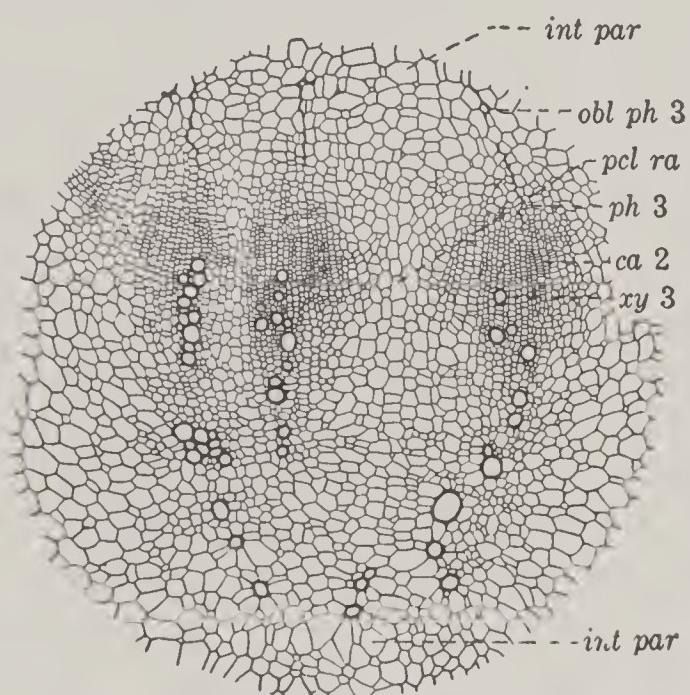


FIG. 133. Sector of large bundle from fourth ring: $ca\ 2$, secondary cambium; *int par*, interzonal parenchyma; *obl ph 3*, obliterated tertiary phloem; *pcl ra*, pericyclic ray; *ph 3*, tertiary phloem; *xy 3*, tertiary xylem. (After Artschwager, *Jour. Agr. Res.*)

of the parenchymatous band; and, in this region, the obliterated remains of crushed sieve tubes and companion cells occur. The cambium external to the parenchymatous band contributes an outer zone of xylem parenchyma in which there are scattered vessels.

On the basis of this interpretation, the interzonal parenchyma is made up of three regions: an outer zone of xylem parenchyma; an intermediate one of pericyclic parenchyma; and an inner region of phloem parenchyma. A somewhat different explanation is given by Artschwager (1) in which he states that

"the interzonal parenchyma in its entirety is made up of three regions: an outer zone containing scattered xylem cells, a central purely paren-

chyma zone, and an inner zone containing obliterated phloem. The first two zones have been formed by centripetal growth of the outer ring, while the third zone is the product of centrifugal growth of the older ring."

Tertiary thickening in the hypocotyl is like that described for the fleshy portion of the root except that the initial secondary cambium is pericyclic in origin rather than arising in the phloem parenchyma. The central portion of the axis consists of a pith which widens out toward the crown stem, and the hypocotyl may become hollow at its upper limit. A union of rings occurs in the upper hypocotyl which is related to the manner of the insertion of the leaf traces in which the bundles of each leaf trace extend inwardly for different distances, the median bundle of each trace reaching the center of the axis while the lateral bundles differentiate centripetally for shorter distances. This vascular arrangement, together with the anastomosing of the annular rings, results in an interconnection between all of the leaves of the rosette and all of the rings of the fleshy axis.

THE FLORAL AXIS. — Slightly below the growing point of the floral axis, a circular zone of procambial tissue is formed which separates the included pith from the cortex. In this zone, collateral vascular bundles are differentiated, the first elements formed being narrow, thin-walled phloem cells which are difficult to distinguish until they are nearly mature. Protoxylem elements of a loose spiral type are next formed and finally, in the intervening zone of procambial tissue, a fascicular cambium arises which produces secondary xylem and phloem. The cortex is parenchymatous, except for ridges of collenchyma near its periphery; and the epidermis is single-layered.

At this stage, the floral axis is roughly polygonal in outline and there are five large caudine bundles at its angles, with numerous smaller bundles in the intervening sectors of the vascular ring. After the fascicular cambium has functioned for some time in the usual manner, an interfascicular cambium is differentiated which is oriented in a way that is unlike the arrangement found in most stems. One arm of the interfascicular cambium is continuous with the fascicular cambium, while the other may arch around outside the phloem of the adjacent bundle so that a unilateral connection with the fascicular cambium, rather than a bilateral one, results. This method of development produces an

undulating zone of cambium which connects some of the bundles directly, and passes outside of others, and the latter may be separated from the subtending cambium by several layers of parenchymatous cells.

As the activity of the anomalous interfascicular cambium proceeds, a secondary cambium arises in the pericycle. This at first produces only xylem elements and parenchyma by centripetal divisions; but, later, it forms groups of phloem and parenchymatous cells centrifugally. Finally, at the points of phloem formation, the secondary cambium becomes inactive and is itself differentiated into vascular tissue and parenchyma. This results in a discontinuity of the extrafascicular or pericyclic cambium, but new segments of secondary cambium appear on the outer face of the extrafascicular phloem which become confluent with the older persistent segments of pericyclic cambium, thus restoring the continuity of the cambial ring. This cambium may then undergo reciprocal divisions producing xylem and phloem tissue.

As a result of this anomalous type of secondary thickening, several systems of mechanical tissue are laid down. (1) The peripheral portions of the primary bundles are bounded by a zone of thick-walled cells in which scattered groups of phloem are located. The cells are not true xylem, except at points immediately centrad to the phloem groups, but form connective or conjunctive tissue consisting of cells which may be parenchymatous or prosenchymatous. (2) The extrafascicular or secondary cambium forms an irregular series of vascular bundles which are surrounded by thick-walled mechanical tissue. (3) The outer zone of the pericycle, from which the secondary cambium originates, is delimited by sectors of lignified fibers. (Fig. 134.)

In summary, there are three phases of cambial activity with respect to the secondary and tertiary thickening of the floral axis and vegetative stem: (1) the production of a normal fascicular cambium which produces phloem and xylem in the usual manner; (2) the formation of an interfascicular cambium which forms unilateral connections with the fascicular cambium; and (3) the development of a secondary or pericyclic cambium, sometimes referred to as extrafascicular, which produces both xylem and phloem elements. Xylem and parenchyma are first produced centripetally by the pericyclic cambium, followed by the centrifugal formation of phloem and parenchyma. Ultimately, sectors of the extra-

fascicular cambium become inactive and differentiate as vascular tissue or parenchyma; but the continuity of the extrafascicular cambial ring is reestablished by the formation of new sectors of

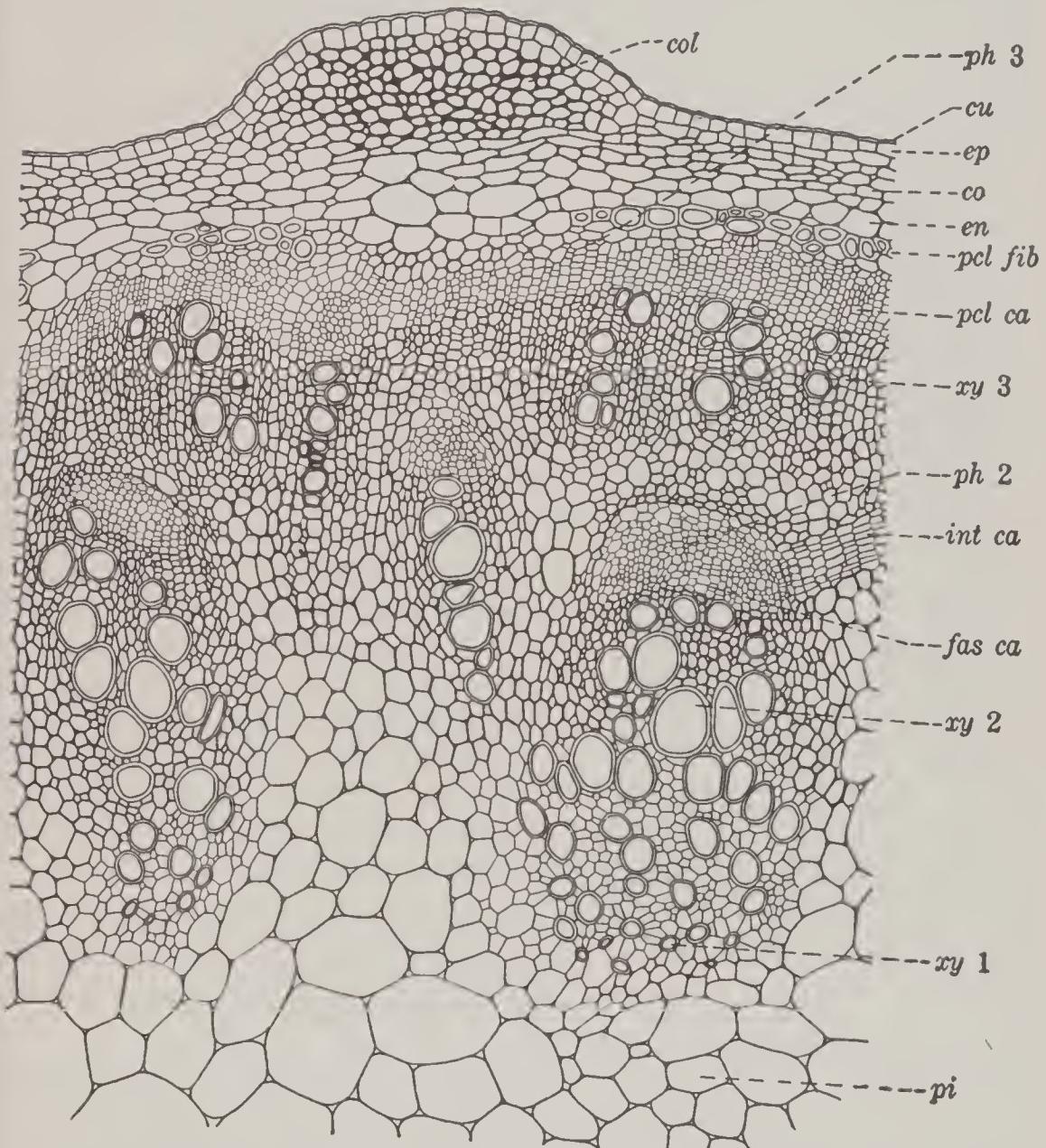


FIG. 134. Transection of portion of stem showing development of secondary and tertiary tissues: *co*, cortex; *col*, collenchyma; *cu*, cuticle; *en*, endodermis; *ep*, epidermis; *fas ca*, interfascicular cambium; *int ca*, pericyclic fiber; *pb 2*, pericyclic cambium; *pcl ca*, secondary phloem; *pcl fib*, primary phloem; *pi*, pith; *xy 1*, tertiary xylem; *xy 2*, secondary xylem; *xy 3*, primary xylem.

cambium from the pericyclic cells located on the outer face of the last-formed phloem. This type of axial thickening continues as long as the stem lives.

THE COURSE OF THE BUNDLES IN THE STEM. — The phyllotaxy of the floral axis is usually alternate with a $\frac{2}{5}$ divergence, although

the lower leaves may appear to be in approximate pairs. The trace of each young leaf consists of a large median bundle and two smaller lateral ones, but at maturity this number is considerably increased so that there are several bundles in the semicircular base of the petiole at its point of divergence from the stem. The course

of the bundles in the Chenopodiaceae and in the genus *Beta* has been investigated by Fron (8), Wilson (21), Artschwager (2), and others. The accounts are in agreement except for differences in the course of the median bundle as reported by Fron who worked with *Beta cyclo*. Artschwager's report, based on *Beta vulgaris*, is here given in part:

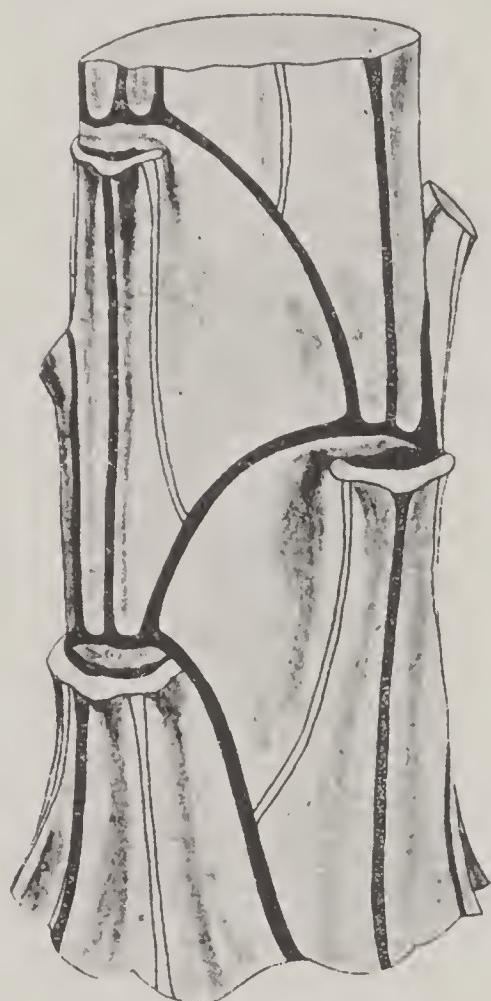


FIG. 135. A portion of floral axis five internodes in length showing vascular anatomy. Cauline bundles are solid black, median traces of leaves are stippled, and lateral bundles of leaves are white. (Redrawn after Artschwager, *Jour. Agr. Res.*)

it ascends without fusion or forking for five internodes and passes into the leaf without branching. The left lateral trace is derived from the caudine bundle next it, passes through three internodes, and usually branches several times before entering the leaf. The right lateral trace is also derived from its adjacent caudine bundle. It passes through only two internodes, but otherwise conforms to the left lateral trace. The length of the lateral trace is, however, subject to variation since it often remains a part of the caudine bundles for a longer or shorter portion of their ascent.

"Occupying the corners of the irregular polygon are five large caudine bundles alternating with an equal number of strands, usually somewhat smaller in size, which represent the median traces of the first five leaves. Flanking the sides of the caudine bundles are small strands of vascular tissue which represent the lateral traces." (Fig. 135.)

Considering only the three main bundles of each trace and disregarding variations which occur,

"the derivation of the traces accords with the following plan. Each new median trace is derived from a left caudine bundle (viewed from the stem apex) a little distance above the node,

"In each node, then, the caulin bundles flanking the oldest median trace undergo the following changes: A little distance below, or sometimes above the insertion of the leaf each caulin bundle gives off a small branch which becomes a new lateral trace; a little higher up they approach each other and may even temporarily fuse. Upon separation, the left caulin bundle branches once more and the new strand which is segregated becomes a new median trace. . . . The vascular supply of the axillary members is also derived from the caulin bundles a short distance below the node."

THE LEAF. — In transection, the petiole is roughly triangular with a trough-like depression along its adaxial surface, but its basipetal portion is wide and more or less flattened. At the base of the lamina, the petiole broadens out and forms wing-like projections which are continuous with the blade. The number of bundles in the petiole varies depending upon the development of the leaf, and it decreases toward the blade as a result of anastomoses of the smaller ones. The large bundles extend the entire length of the petiole and are reinforced by crescentic strands of mechanical tissue which lie immediately outside the phloem and to a lesser degree adjacent to the xylem. The petiole is further strengthened by zones of collenchyma located just within the epidermis which are so distributed that they form projecting ridges on the abaxial surface of the petiole and a band several cells in width in the hypodermal region of the adaxial surface.

The epidermal cells are somewhat elongated and there are numerous stomata except in regions overlying the collenchymatous strands. The hypodermal cells may contain anthocyanin, and chloroplasts are present in the compact outer layers of parenchyma and to some extent in the more spongy central parenchyma. The bundles are collateral or occasionally half-amphivasal. The phloem consists chiefly of sieve tubes and companion cells with some parenchyma, while the xylem is comprised of primary and secondary vessels with both thin- and thick-walled fibers.

The epidermal cells of the blade are polygonal in surface view with sinuous walls and the stomata are simple without accessory cells, each pore being surrounded by a pair of guard cells containing several chloroplasts. The stomatal counts which have been recorded indicate a great variation in the absolute number per unit area, probably due to differences in variety and in the condition of the leaf at the time the count was made. Sixteen counts, made by Artschwager (1), of leaves of varying size and color gave an

average of 99 per sq. mm. in the upper epidermis and 121 in the lower.

The mesophyll is chlorenchymatous and rather compact with no sharp differentiation between the palisade and spongy tissue. There is apparently a correlation between the thickness of the leaf and the character of the mesophyll cells; and Artschwager found that in thick leaves, practically all of the cells are of the elongated palisade type, while in very thin leaves, the entire mesophyll consists of relatively short, round cells. The main veins are like those of the petiole and are reinforced by zones of collenchyma which abut both epidermal layers, the more extensive abaxial zone being several layers in width.

In connection with investigations of the curly-top disease in the sugar beet, Esau (7) has studied the ontogeny of the phloem in the leaves. The sieve tube and its companion cell arise from the mother cell by a longitudinal division. The daughter nuclei in the two cells are unlike, that of the companion cell being more granular and deeply staining. (Fig. 136, 4.) The cytoplasm is vacuolate, the vacuoles being numerous and small in young primary phloem cells, and large and relatively few in number in young secondary phloem cells. (Fig. 136, 4 and 2.) As the sieve tube develops, characteristic slime bodies form which are plastic and shaped like irregular drops. These are regarded as inclusions of proteinaceous material which later disintegrate and become a part of the vacuolar substance in mature sieve tubes. A very characteristic feature of the phloem is the development of plastids in the sieve tube and companion cell. These are commonly disk-shaped, but sometimes appear as thick rings with a clear area in the center. The plastids persist as permanent cell organs and are at first scattered throughout the cytoplasm, later accumulating in greater numbers near the sieve plates. (Fig. 136, 2.) As the sieve tubes mature and later become crushed, the plastids begin to disintegrate, this process being initiated by swelling.

The nucleus of the sieve tube disintegrates during its maturation at about the time that the slime bodies break down. The walls of the tube thicken perceptibly, especially in the primary phloem, and the areas where the sieve perforations develop can be detected at about the time that the slime bodies are formed. (Fig. 136, 1.) Later, the plate thickens, the pores become distinct, the sieve element attains its full length, and the tube may be regarded as mature.

Senility is indicated by the formation of definitive callus on the sieve plates; and, eventually, the tube is crushed. (Fig. 136, II.)

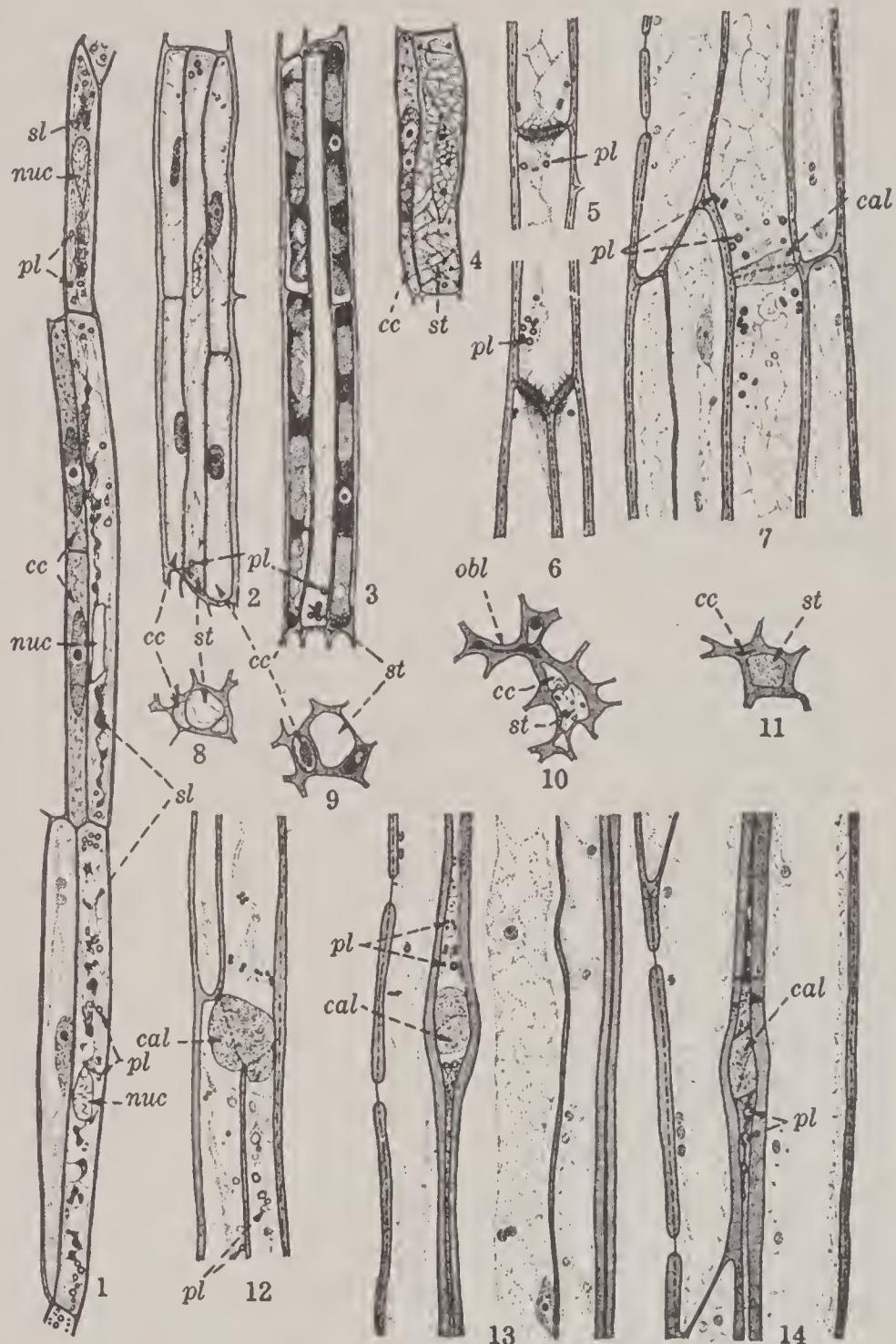


FIG. 136. Ontogeny of sieve tubes in leaf of sugar beet. 1, young sieve tube with slime bodies, plastids, and disintegrating nuclei; 2 and 8, younger; 3 and 9, older sieve tubes and companion cells from secondary phloem; 4, young sieve tube and companion cell from primary phloem; 5 and 6, portions of mature sieve tubes showing primary lamellae and secondary thickenings on sieve plate, slime accumulations, and plastids; 7 and 12, definitive callus on sieve plates, plastids, and cytoplasmic network of old sieve tubes; 10, sieve tube and companion cell in early stage of obliteration and two crushed cells; 11, crushed sieve tube and companion cell; 13 and 14, two stages in obliteration: *cal*, callus; *cc*, companion cell; *nuc*, nucleus; *obl*, obliterated cells; *pl*, plastid; *sl*, slime bodies; *st*, sieve tube. (After Esau.)

The companion cells are frequently divided transversely, especially in the secondary phloem, so that there may be two to a sieve tube. Another variation occurs when the mother cell divides more than once longitudinally, forming two companion cells and one sieve tube. The former may divide transversely so that four companion cells abut one sieve element. Chloroplasts occur in the cytoplasm which is vacuolate. The phloem parenchyma is not

specialized; and frequently exhibits meristematic potentialities in general cell division and in cambium formation, as it does in the root and stem.

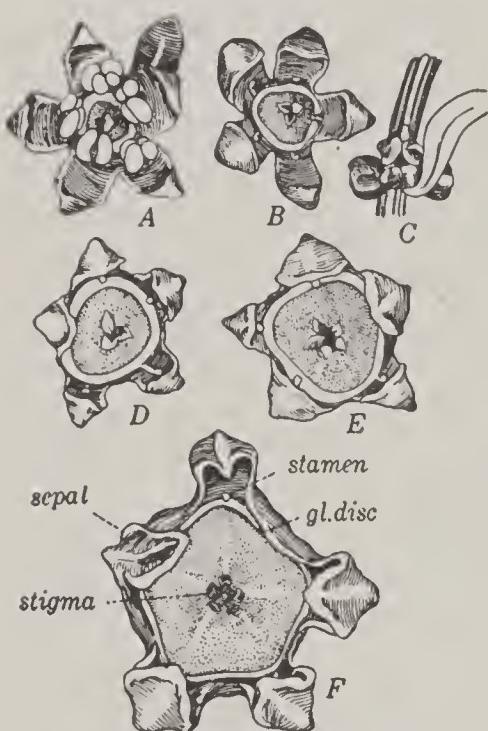


FIG. 137. *A*, single mature flower viewed from above; *B*, flower with stamens already dropped; *C*, cluster of flowers attached to branch of inflorescence axis and subtended by bract; *D*, flower after fertilization; *E*, flower with young embryo; *F*, flower with mature embryo: *gl. disc*, glandular disc. (After Artschwager, *Jour. Agr. Res.*)

may be two, four, or five. The half-inferior ovary is sunken in a fleshy disk, and the very short style is terminated by two to five awl-shaped stigmas. A single campylotropous ovule is attached laterally to the ovary wall by a short funiculus.

Payer (14) studied the floral development of *Beta maritima* and the development in the sugar beet as reported by Artschwager (2) agrees with it in all essential details.

"The rudiments of the young flowers appear close behind the growing points of branches of the inflorescence axis. Each rudiment is borne in the axil of a large bract and is accompanied by two lateral bracts

each of which has in its axil a flower. The flower primordium forms a small protuberance on which are soon differentiated five narrow ridges, the beginnings of the sepals. Next there appears within this circle a whorl of papillae, the stamen rudiments, each opposite a calyx lobe. Finally, three more ridges develop at first separately; but later joining to inclose a more or less compressed roundish cavity in which a single ovule develops.

"Once initiated, the primordia of the different floral parts develop very rapidly. The young stamens become stalked early and attain in cross section the characteristic quadrilocular form. The anther is at first a homogeneous mass of tissue covered by an epidermis. As soon as it becomes faintly 4-lobed in cross section the cells next to the epidermis begin to elongate radially and divide periclinally, forming two layers of narrow cells which by their size and staining reaction appear distinctly set off from the central tissue which forms the archesporium. These two layers of cells together with the epidermis constitute the anther wall. The cells of the middle layer, in their subsequent development, enlarge rapidly and finally develop thickening bands. This constitutes the endothecium and forms a continuous mantle except in the region where the anther later dehisces. . . . The cells remain small and as the anther enlarges they become stretched tangentially, but they do not become obliterated before the endothecium is fully developed and the pollen practically mature.

"The ovule arises near the base of the carpels. It is seen first as a slight protuberance which enlarges to form the nucellus. In its subsequent development the young ovule becomes distinct from the surface of the carpel by a stalklike base or funiculus. Very early there appears at the base of the nucellus an annular outgrowth followed soon by a second one of a similar nature. The first outgrowth develops into the inner, the second into the outer integument. The young ovule is straight, but with the appearance of the integuments it curves and becomes campylotropous. Finally, the ovule twists about its own funiculus and comes to lie horizontally in the cavity of the ovary."

At the base of the receptacle, the vascular traces of the floral organs form a short stele which is a somewhat irregular central core rather than a dissected siphonostele. Five distinct groups of vascular units diverge in the broader portion of the receptacle occupying a peripheral position in the cortical zone, and the remainder of the central core forms a single bundle which is continuous with the vascular supply to the ovule. (Fig. 138, A.) The vascular strands which diverge from the cortical region pass out into the five calyx lobes, and each of these bundles later gives off branches to form the lateral traces of the lobes. (Fig. 138, C.) The pistil, which consists normally of three undiverged carpels,

occupies the central portion of the flower; and, although carpels are commonly supplied with three bundles (a central bundle and two marginal ones), in this instance the marginal bundles have been suppressed, and each carpel is supplied by a single vascular strand. The carpillary bundles are derived from the cortical

bundles of the receptacle, and are so differentiated that two of them constitute direct branches of two of the cortical bundles which lie opposite them while a third carpillary bundle is the product of a fusion of two vascular strands derived from adjacent cortical bundles. In some instances, these two bundles remain distinct so that the upper part of the pistil may contain four bundles instead of three. After the divergence of the vascular strands to the sepals and carpels from the cortical bundles, the distal sections pass out into the stamens, each being supplied by a single bundle. (Fig. 138, D.)

MICROSPOROGENESIS.—

Microsporogenesis follows the general sequence that occurs in many angiosperms, although Matthysen (12) has noted some differences in the early prophases; and the sporogenous tissue of the young anther develops rapidly to the mother cell stage. Each pollen grain contains nine chromosomes, which is the haploid number reported for the genus and for many other members of the Chenopodiaceae. Matthysen reports finding eight chromosomes for the cultivated garden beet; but this

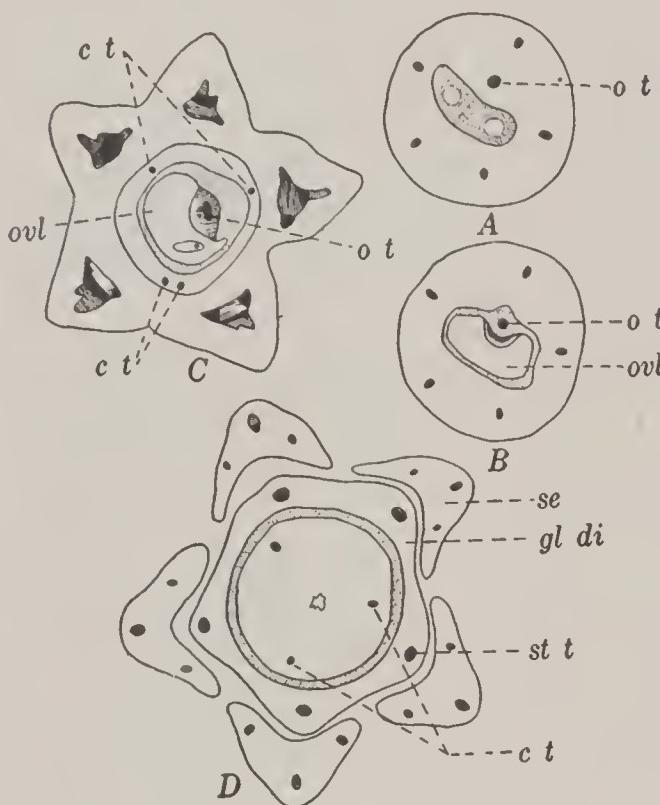


FIG. 138. Diagrammatic series of sections through flower to illustrate origin and course of vascular supply; A, section through base of receptacle showing five peripheral bundles and sixth one ($o t$) in close proximity to base of ovary cavity; B, section taken at slightly higher level, bundle ($o t$) forms vascular supply of single ovule (ovl); C, section at level where sepals are differentiating and peripheral bundles are branching. Four strands designated ($c t$) form vascular supply of three carpels; D, section through upper part of flower showing distinct sepals (se). The filaments of stamens are still part of glandular disk region ($gl di$). Each stamen is supplied with a single trace ($st t$). (After Artschwager, *Jour. Agr. Res.*)

Matthysen (12) has noted some differences in the early prophases; and the sporogenous tissue of the young anther develops rapidly to the mother cell stage. Each pollen grain contains nine chromosomes, which is the haploid number reported for the genus and for many other members of the Chenopodiaceae. Matthysen reports finding eight chromosomes for the cultivated garden beet; but this

is the only notable exception to the findings of Winge (22) and Heel (9).

Since microsporogenesis proceeds at a more rapid rate than megasporogenesis in any given flower, it is probable that the individual flowers of a cluster are not ordinarily self-pollinated. The mature pollen grain has a thick, sculptured outer wall with many thin spots or germ pores, one of which serves as the point of emergence of the pollen tube. The division of the microspore nucleus to form the tube nucleus and the two microgametes occurs several days before the liberation of the pollen. Prior to dehiscence, there are also small irregular starch grains in the microspore which disappear before the pollen is shed. There is a considerable amount of pollen degeneration, but Artschwager and Starrett (3) find that, in most cases, more than one pollen tube reaches the megagametophyte. These grow down the stylar canal, and fertilization may be effected in 20 hours or less.

MEGASPOROGENESIS. — In megasporogenesis, the archesporium is formed from a single hypodermal cell of the nucellus; and subsequent periclinal divisions of epidermal cells result in the embedding of the megaspore mother cell more deeply in the nucellar tissue. The meiotic divisions produce a linear tetrad of megaspores, the outer three of which degenerate while the inner one is functional. The orientation of the megagametophyte is at first straight; but changes in the position and content of the nucellar cells, together with their unequal growth rate, result in curvature; and further divisions of the nucellar cells produce the tissue which ultimately forms the perisperm of the mature seed. (Fig. 120.)

The development of the megagametophyte follows the usual program. There are three successive equational divisions of the megaspore nucleus producing eight free nuclei. Of these, the egg, or megagamete, and two synergids are located toward the micropyle; the two polar nuclei unite to form the primary endosperm nucleus, which is usually centrally located; and the three antipodal cells are at the chalazal end. There may be more than three antipodals which persist for several days after fertilization and then disintegrate.

EMBRYOGENY. — At the time of fertilization, the ovule is small; but later it grows rapidly and attains mature size before the embryo within is fully developed. During this period of growth, the calyx also enlarges and its lobes curve back to the position held at anthe-

sis. The zygote undergoes a period of rest, then divides transversely, and the two daughter cells again divide in the same plane so that a linear tetrad of cells is formed. Of these, the basal one gives rise to the suspensor and the other three produce the embryo proper. Artschwager and Starrett (3) have described the subsequent stages in the embryogeny and point out that "after the formation of the quadrant, no strict law governs the sequence of cell division"; although "a certain balance seems to be maintained so that the final product is remarkably uniform."

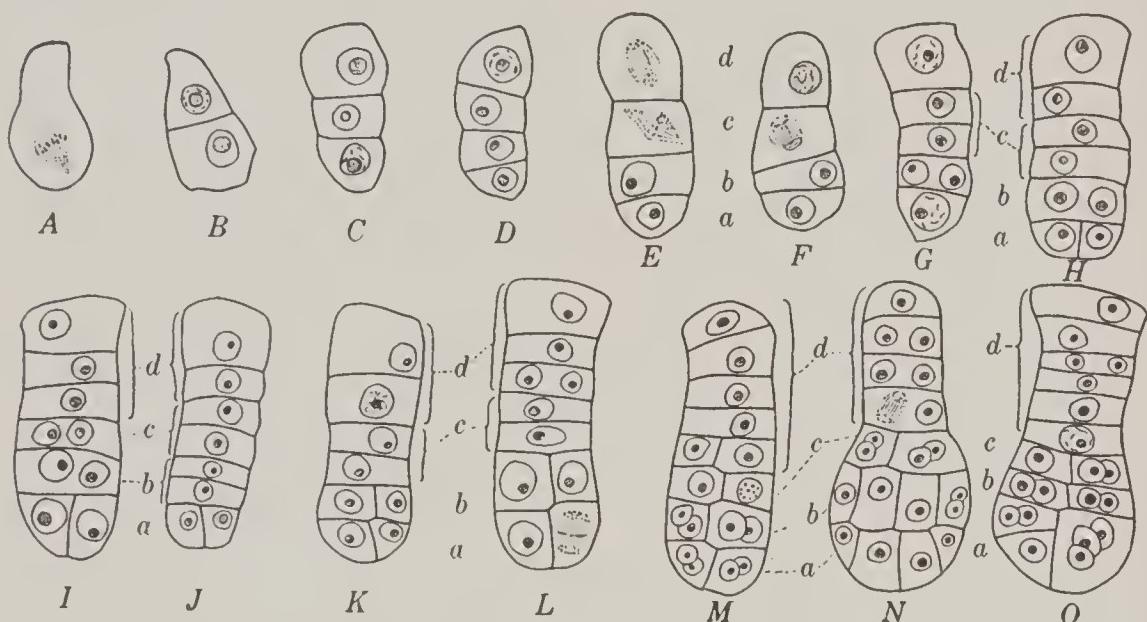


FIG. 139. *A-O*, series of diagrammatic drawings showing sequence of cell division in development of young embryo. Cell *a* represents apical cell of tetrad and cell *d* basal one. (Redrawn after Artschwager and Starrett, *Jour. Agr. Res.*)

In most cases, each cell of the tetrad divides once to form an eight-celled embryo. Cell *d* usually divides first, followed by cell *c*, or they may divide simultaneously; and this is also true of cells *a* and *b*. (Fig. 139.) Cell *a* always divides vertically; but *b* may divide either vertically or transversely, and this is the case with cell *c*, so that the octant stage may be five, six, or seven tiered. Subsequent divisions produce the 16-celled embryo which, like the octant, varies in its number of tiers depending upon the plane of the division walls. At this time, the embryo begins to be club-shaped; and, in about five days, becomes globular. The cotyledons are differentiated approximately two days later and the embryo is usually mature by the twelfth to fourteenth day.

Concurrent with the development of the young embryo; there is free nuclear division of the endosperm nuclei which occupy a

peripheral position in the embryo sac. Wall formation follows, and, finally, the entire sac is filled with storage cells which are later resorbed by the growing embryo except for a single layer surrounding the hypocotyledonary portion of the embryonic axis. This persistent layer consists of small, very regular cells with dense contents. At the time that the curved embryo sac has reached its final form and size, the peripheral layer of nucellar tissue is four to six cells in thickness; but as the embryo enlarges, the inner peripheral layers are gradually resorbed. The remaining cells of the perisperm ultimately become packed with large starch grains except in the chalazal region.

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CHAPTER X

CRUCIFERAE

RAPHANUS SATIVUS

THE mustard family is large and its members widely distributed. It includes several species of economic importance and numerous common weeds. These are chiefly herbaceous with a pungent watery juice, simple alternate leaves that are variously lobed and dissected, and flowers that are regular, perfect, and cruciform. The fruit is a pod-like structure known as a silique which is usually dehiscent. Among the more widely cultivated crucifers are radish, *Raphanus sativus* L.; cabbage, *Brassica oleracea*, var. *capitata* L.; cauliflower, *B. oleracea*, var. *botrytis* L.; Brussels sprouts, *B. oleracea*, var. *gemmifera*, Zenk.; turnip, *B. rapa*, L.; mustard, *B. nigra* (L.) Koch., and *B. alba* (L.) Boiss.; rape, *B. Napus* L.; and horseradish, *Radicula Armoracia* (L.) Robinson.

GENERAL MORPHOLOGY

The radish is extensively cultivated as a garden crop and grows as an herbaceous annual or a true biennial in northern climates. It normally produces a fleshy tap root and a rosette of leaves the first year; but, when planted early, may form the flower and fruit the same season. (Fig. 140.) Radishes may be classified on the basis of their time of maturation; and, with respect to seasonal development, there are early or forcing varieties, summer, and winter types. The early varieties are the most commonly planted and are often grown in hot beds and greenhouses, frequently reaching marketable size in from 20 to 30 days. The quickly maturing types, including the Scarlet Globe variety upon which the present studies are largely based, remain tender and succulent for a short time only. Summer radishes require six to eight weeks to mature and are larger than the early types. The winter varieties, which

need several months to reach maturity and often attain a large size, have a compact, firm flesh and can be successfully stored for some time.

THE ROOT. — The root and hypocotyl constitute the succulent portion of the plant which is generally eaten in the fresh state. This fleshy axis is variable in size, shape, and color depending upon the variety. The shape may be spherical, bluntly cylindrical, or



FIG. 140. Radish plant in seed. (Courtesy Ferry-Morse Seed Co.)

conical and much elongated; and the color ranges from cream-white, pink, red, and variously mottled combinations to gray or even black.

Weaver and Bruner (20) have pointed out that the development of the root system is of an entirely different character in the round or turnip-shaped varieties than in the half-long or long types. The former are characterized by a rapidly growing tap root which may penetrate the soil to a depth of 2 to 3 feet with a lateral spread of 12 to 16 inches. Most of the absorbing area lies in the upper 2 to 8 inches of surface soil; and, even in fully matured plants, only the portion of the tap root occupying the first 2 to 12 inches of surface

soil produces large laterals. These may extend horizontally to distances of 3 feet or more on all sides of the plant, branching profusely and forming a network of rootlets. In the Long Scarlet type, by the time the upper portion of the root has reached marketable size, it may have penetrated to depths of 3 feet with much-branched laterals which spread radially to distances of 2 feet. The mature plants are characterized by tap roots $4\frac{1}{2}$ to 5 feet long with many major laterals in the surface foot of soil which frequently extend outward to a maximum of 40 inches. They in turn may give rise to branches which penetrate the soil deeply; and, as a result, the surface soil is well filled with roots while the subsoil also contains numerous branched laterals.

THE HYPOCOTYL. — The upper portion of the fleshy primary axis is practically devoid of lateral roots, consisting of a thickened hypocotyl which is transitional in its vascular organization. The relative proportion of the lower part of the axis which can be regarded as the root is greater in the case of the half-long or long icicle varieties than in the globe types. Golinska (6) interprets the fleshy portion as a transition region and regards it as being more root-like than stem-like. (Fig. 141.) There is a reorientation of the vascular elements in the upper limits of the hypocotyl, but the endarch relationship is not attained at the cotyledonary node, and exarch strands extend into the cotyledons as in the potato.

Although it has been demonstrated genetically by Malinowski (10), Moldenhawer (12), and Sutton (19) that the development of the fleshy axis is a hereditary characteristic, external factors, especially length of day, have a marked influence upon the degree of its development. Sinskaja (17) found that varieties brought from China, Mongolia, Japan, and India produced no thickenings and bloomed the first year when grown in greenhouses in Leningrad; but when the photoperiod was reduced to an interval of 7 to 12 hours, they became fleshy and bloomed much later or not at all. Garner and Allard (5) obtained fleshy root-hypocotyl axes with a 7-hour day, and with a 12-hour day were able to produce seeds in the winter months.

THE STEM. — There are two phases in the development of the stem. The first occupies the initial 4 to 6 weeks after germination when a rosette of leaves develops from a short crown stem. The second period is that during which the flower stalk is formed fol-

lowing the vegetative period. The axis elongates at this time to produce an erect, much-branched stem which may attain a height of 1 to 3 or more feet. It is usually somewhat glaucous, sometimes sparsely pubescent with a few stiff epidermal hairs on the lower portions of the stem system; and, in rare instances, is essentially glabrous throughout. (Fig. 142, A.)

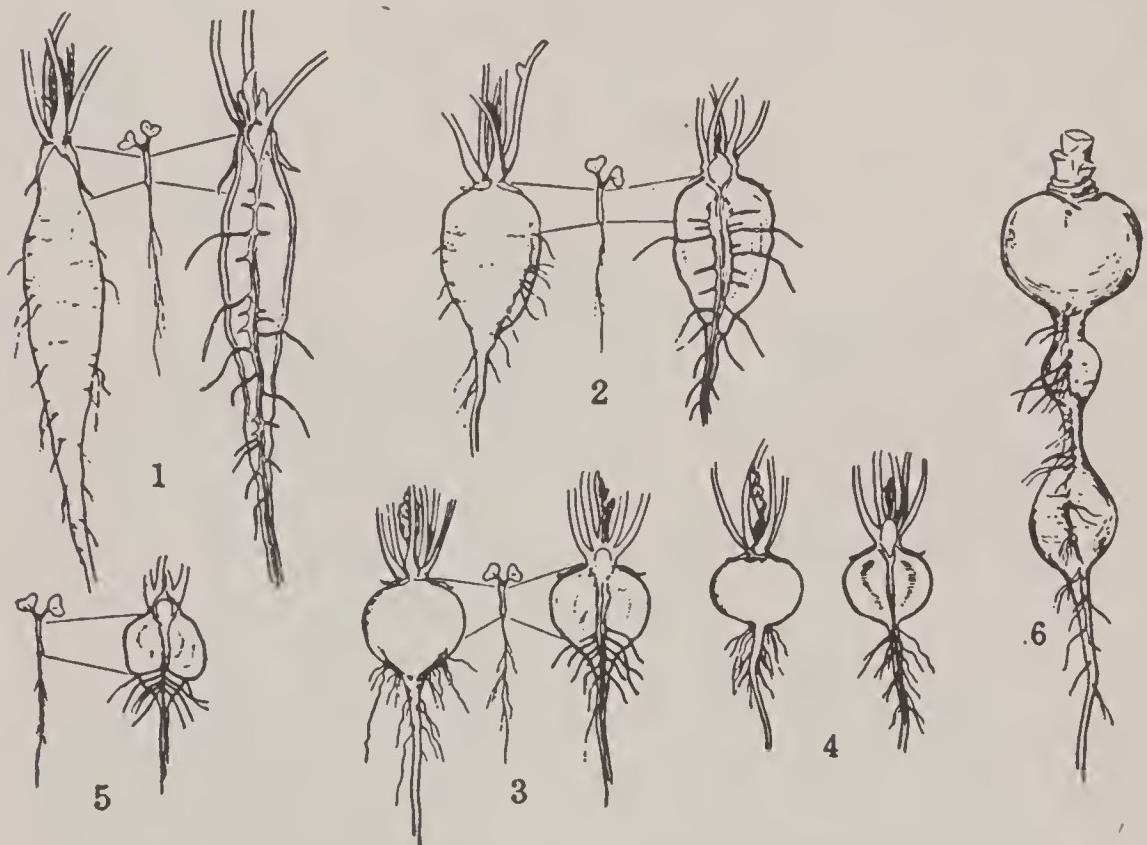


FIG. 141. Development of fleshy axis of *Raphanus* in icicle, 1, half long, 2, and globe types, 3-5, showing region that becomes fleshy and origin of secondary roots; 6, abnormal thickening of axis. (After Golinska, *Die Gartenbauwissenschaft*.)

THE LEAVES. — The simple petiolate leaves are glabrous or sparingly pubescent and are spirally arranged in a $\frac{2}{5}$ phyllotaxy. They are variable in shape, the smaller upper ones being more or less oblong while the lower ones are deeply lyrate-pinnatifid.

THE INFLORESCENCE AND FLOWER. — The inflorescence is an elongated raceme which is ordinarily devoid of bracts, and the white or rose-lilac flowers are borne on slender pedicels. (Fig. 142, A.) The pentacyclic flower is hypogynous. It consists of a calyx of four sepals, a corolla with a similar number of petals, six stamens in two cycles, and a pistil that has been interpreted as consisting of four carpels by some investigators and of two by others. (Fig. 143, A.)

The four sepals are paired. The outer median pair slightly

overlap the inner pair in the bud stage, and are somewhat more beaked at their apices, which commonly bear a few prominent hairs. The four petals are alternately arranged with respect to the sepals and their spreading limbs form a cross. The stamens are arranged in two cycles, the outer consisting of two functional stamens which are shorter than the inner ones, and two rudimentary or vestigial stamens which develop as small knob-like, or slightly



FIG. 142. A, habit of inflorescence; B, single flower; C, same, in partial face view; D, petal; E, stamens and pistil with perianth removed; F, receptacle with perianth and two of inner stamens removed showing one rudimentary outer stamen and location of nectaries.

elongated, protuberances. The members of this whorl lie alternate to the petals and opposite the sepals. Adaxial to and at the bases

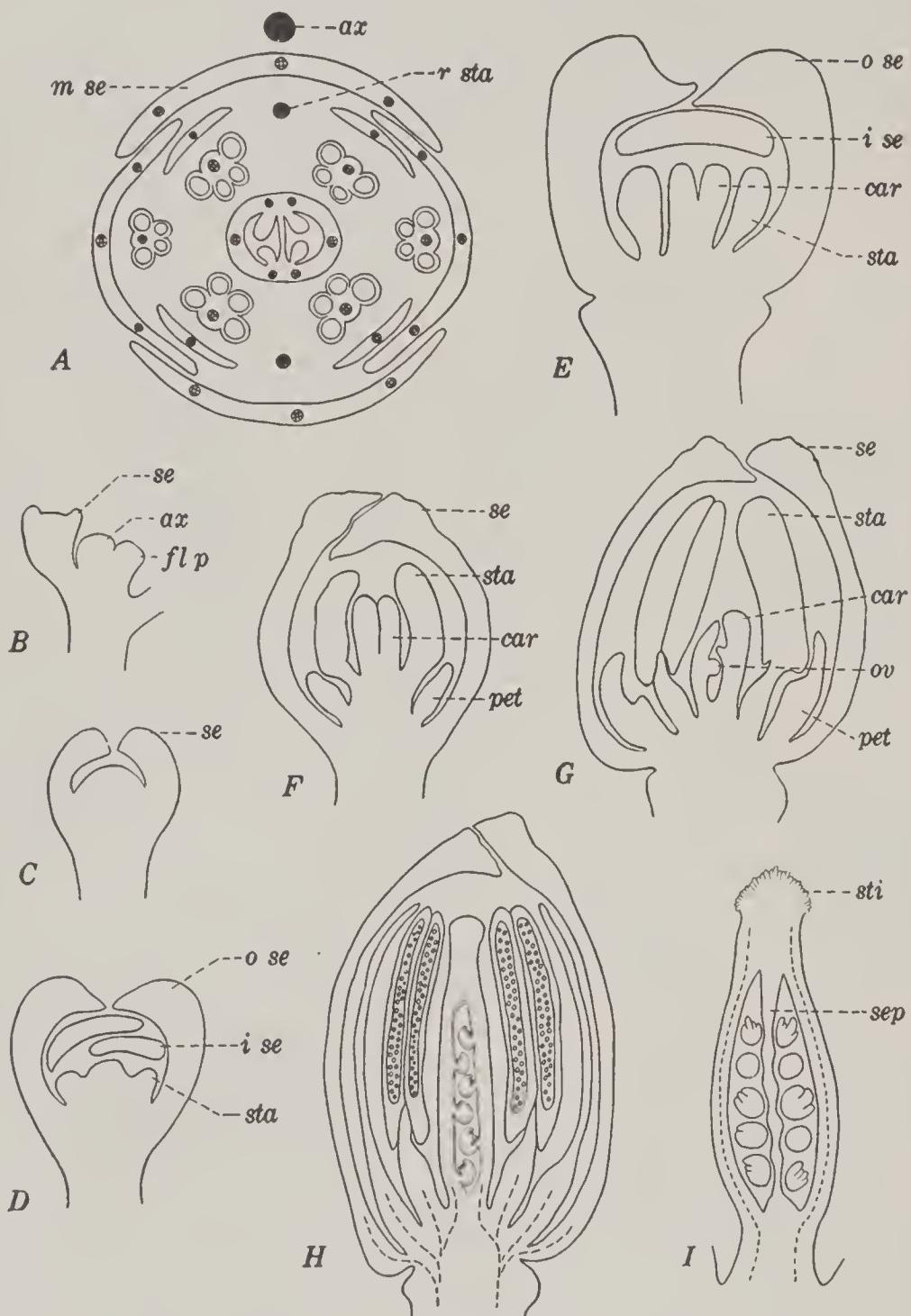


FIG. 143. Floral development: *A*, semi-diagrammatic transection of young flower showing its relation to axis and arrangement of floral parts; *B*, longisection of terminal portion of axis of inflorescence showing origin of flower primordia; *C-H*, longisections of stages in development of flower; *D* and *E*, sections which pass through median or outer pair of sepals and include segments of inner pair (*G* and *H* are oriented in plane parallel to septum of ovary); and *I*, longisection of ovary at right angles to septum (points of divergence of ovules are not shown in this plane): *ax*, axis; *car*, carpel; *fl p*, flower primordium; *i se*, inner sepal; *m se*, one of the median or outer sepals; *o se*, outer sepal; *ov*, ovule; *pet*, petal; *r sta*, rudimentary outer stamen; *se*, sepal; *sep*, septum; *sta*, stamen; *sti*, stigma.

of the two functional stamens are the nectaries. (Fig. 142, F.) There are four equal stamens in the inner whorl which lie opposite the petals. The anthers of the functional stamens are two-loculed at maturity and longitudinally dehiscent.

The pistil has been interpreted as consisting of four carpels by Eames and Wilson (2, 3). Based upon the character of the vascular supply of the ovary, they state that

"it appears that there are four carpels in the Cruciferae instead of two, the generally accepted number. Two of these carpels are valve-like and sterile and are placed below two other carpels, nearly enclosing them. This second set of carpels, the fertile or 'solid' carpels, is reduced; the loculus has disappeared, and the ovules borne by these carpels have been forced out of the loculus and lie in the loculus of the valve, or sterile, carpels. This has taken place phylogenetically, not ontogenetically."

Saunders (15, 16) also describes the gynoecium of the crucifers as consisting of four carpels and presents the concept of carpel polymorphism to explain the occurrence of different combinations of various carpel types, stating that "when the median carpels become solid the characteristic form is a siliqua, when they become semi-solid the result is a silicula."

A somewhat different interpretation of the relationship of the floral parts is presented by Eichler (4), and this has been accepted at least in part by Sachs (14) and Strasburger (18). In the Eichler system, the typical cruciferous flower is described as consisting of two lower median sepals, two upper lateral sepals, four diagonal petals in one whorl, two lower lateral stamens, two upper median stamens, and two lateral carpels. The cycle of apparently four inner stamens is regarded as consisting in reality of but two stamens, each of which is branched at its base. This concept of the dimerous symmetry of the flowers of the Cruciferae was carried a step further by some of the early botanists who regarded the four petals as being derived from a single pair by a lateral doubling or branching, in a manner similar to that described for the inner whorl of stamens.

ANATOMY

ONTOGENY OF THE FLOWER. — In the ontogeny of the flower, the origin of the floral parts does not occur in acropetal succession; and like *Capsella*, as described by Coulter and Chamberlain (1), the petals are the last floral organs to be differentiated. The primor-

dium of the flower is diverged from the main axis of the inflorescence as a conical growing point, and shortly thereafter the primordia of the sepals are differentiated.¹ (Fig. 143, B.) The growth of the sepal primordia is differential; and the median pair, which become the outer sepals, grow more rapidly than the lateral ones partly enclosing and overarching them. (Fig. 143, D.) The staminal primordia are next differentiated, followed shortly by the carpels, and lastly by the petals. (Fig. 143, E, F.)

As the carpels develop, a partition is formed which has been termed the dissepiment or septum. In structure this is somewhat variable. At the base of the ovary, it may be thick and solid, while above, it is frequently hollow or double, consisting of two thin walls between which there may be an empty space or some spongy parenchyma. It is thought by some to originate as a secondary placental outgrowth; while others, including Eames and Wilson (2), regard the septum as "an expansion of the ventral margin of the folded solid carpels."

FRUIT AND SEED. — The mature fruit is an elongated, conical pod or silique, 1 to 3 inches in length. It has an extended beak which may equal or exceed the pod itself; and, unlike the majority of cruciferous fruits, is indehiscent. It produces two or three, or sometimes several, seeds which are partially embedded in the spongy tissue of the placentae and septum of the ovary. The ovules are campylotropous, the micropyle being directed toward the stylar end of the ovary. (Fig. 143, H.) The mature embryo is curved and occupies the entire space within the seed coat except for a very small amount of endosperm. The cotyledons are conduplicate, or folded upon themselves and around the embryonic axis, with the outer, larger cotyledon clasping the inner one. (Fig. 145.)

Winton (21) has described several cruciferous seeds, and Kondo (9) has investigated that of the radish in detail. Both agree that the seed coat normally consists of four layers, but Winton states that "in many species the first and second layers at maturity are not distinctly cellular." Kondo's work included about 30 varieties which he divided into three form groups: (1) heart-shaped, (2) type oval or egg-shaped, and (3) long-oval. (Fig. 144, A, B, C.)

¹ The author is indebted to Mr. Charles H. Quibell, who kindly permitted the use of his materials in the preparation of this section and the accompanying figures on floral development.

two is the most common, including the Scarlet Globe and many other leading varieties grown in the United States. The color may be yellow, golden brown, cinnamon, russet, or walnut brown. There is also considerable variation in size, the dimensional range being 3.6 to 4.1 mm. in length, 2.7 to 3.3 mm. in breadth, and 2.1 to 2.3 mm. in thickness.

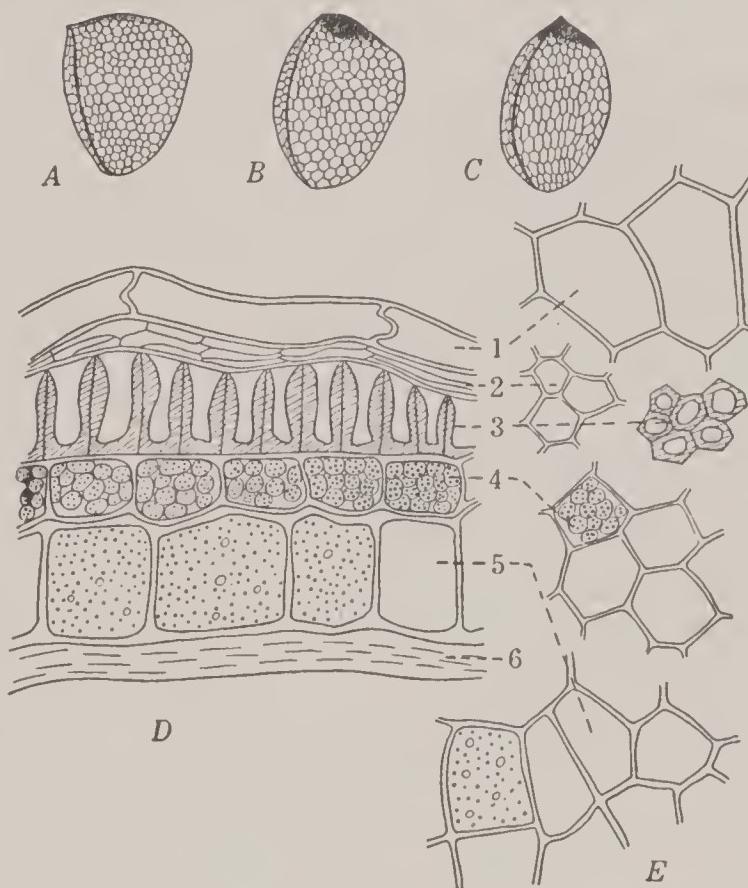


FIG. 144. A-C, three common forms of seed; A, heart-shaped; B, oval or egg-shaped; C, long-oval; D, transection of seed coat and endosperm showing principal layers; E, view of cells of same: 1, epidermis; 2, outer parenchyma; 3, palisade cells; 4, pigment layer; 5, endosperm; and 6, hyaline layer. (Redrawn and rearranged after Kondo, Ohara Institute.)

The outer surface of the seed coat is pitted, and the polygonal reticulations are five or six-sided, varying in degree of prominence and size depending upon the variety. The epidermal layer consists of tabular cells which have thin or sometimes thick, lamellate walls. Underlying them is a subepidermal parenchymatous zone comprised of a series of tangentially oriented cells that are strongly compressed and have thin golden-brown walls. The third zone is made up of palisade cells which form the most conspicuous layer of the seed coat owing to the fact that the inner walls, or at least the inner portion of the lateral walls, are more or less strongly

thickened. They are gold or brown and appear reticulate and sharply polygonal in surface view. (Fig. 144, *D, E.*)

The fourth or pigmented zone is one or more cell layers in thickness and contains the coloring matter of the coat. It consists of much-compressed cells with extremely thin walls, which in some varieties are small, but in others, including the Scarlet Globe, are large and polygonal with an abundant dark-brown pigment.

The remaining layers have been interpreted by some investigators as a part of the inner integument, but Winton and Kondo have demonstrated that they are portions of the endosperm. The aleurone cells of this zone are somewhat similar to those found in the outer portion of the endosperm of cereals. This layer is usually one cell in thickness except in the region of the micropyle, where there may be two or more layers, and adjacent to the hilum where it may be entirely absent. The remainder of the endosperm consists of a hyaline zone made up of several layers of tangentially stretched and much crushed parenchymatous tissue.

DEVELOPMENT OF THE SEEDLING. — The germination of the seed is rapid. Seedlings have been observed with from six to eight laterals on the upper inch of the tap root within four days of planting and before the cotyledons are completely unfolded. At the end of nine days, when the first foliage leaves appear, secondary laterals have been formed. The primary root pushes through the seed coat near the micropyle and elongates rapidly, becoming slightly arched at its upper limits. In the early stages of development, elongation of the hypocotyl and root proceeds much more quickly than in the epicotyl. The growth and straightening of the hypocotyl lifts the conduplicate cotyledons above ground, and they soon expand to form the first photosynthetic organs of the seedling. (Fig. 145.)

ONTOGENY OF THE Root. — The primary root has a diarch protostele. The cells of the two protoxylem points are differentiated centripetally, and with the larger metaxylem vessels toward and at the center, form the complete primary xylem strand. The two groups of primary phloem alternate with the points of protoxylem and are separated from the xylem by a zone of fundamental parenchyma. The pericycle consists of a single layer of cells lying immediately within the endodermis in which Casparyan thickenings are evident by the time the primary xylem is completely matured.

(Fig. 147, A.) The cortex is comprised of a few layers of large parenchymatous cells, and the epidermal cells are also thin-walled, many of them becoming root hairs.

The development of the primary root corresponds to type three as described by Janczewski (8). The terminal meristem of the root is differentiated into three histogens, the calyptrogen-dermatogen, the periblem, and the plerome, each consisting of a single layer of cells. (Fig. 146.) In the ontogeny of the axis, the root cap and epidermis arise from the calyptrogen-dermatogen layer, the cortical cells from the periblem, and the stelar tissue from the plerome.

The root cap consists of several layers of cells which form a series of overlapping cones surrounding the meristematic region of the root tip. As the calyptrogen cuts off successive cell layers to form the root cap, the distal or marginal cells of the conical histogen cease periclinal division and, by continued anticlinal divisions, form the single layer of epidermal cells. This method of differentiation results in an epidermis with a stair-step arrangement in which each step of the epidermis abuts one layer of the root cap cells, rather than an epidermis with a continuous smooth surface. The steps become progressively shorter toward the apex of the root and finally end in one which is a single cell in height, touching the last-formed layer of the root cap. In consequence, the number of steps corresponds to the number of layers of the calyptra, except

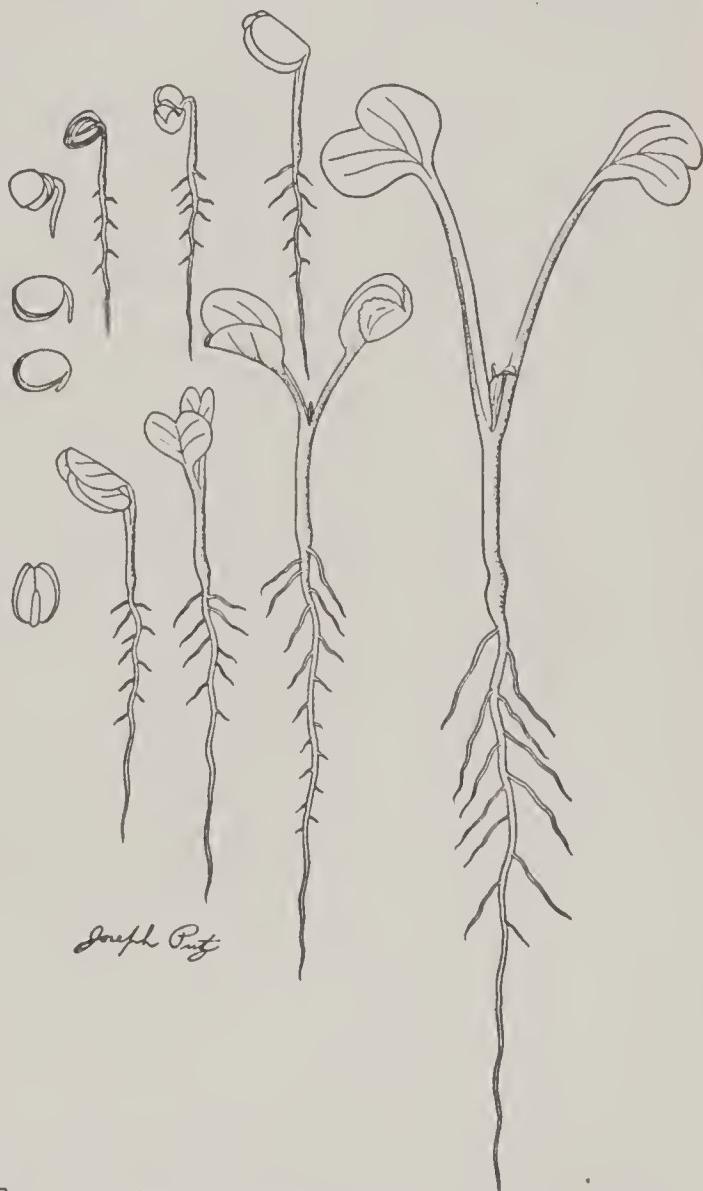


FIG. 145. Stages in development of seedling, variety Red Globe.

where subsequent periclinal divisions of the cells of the calyptra may have occurred. (Fig. 146.)

The cortex originates from the periblem and is composed of large parenchymatous cells whose radial dimensions at first much exceed the axial ones. They decrease in size toward the stele and are limited inwardly by the endodermal layer. This is formed by a

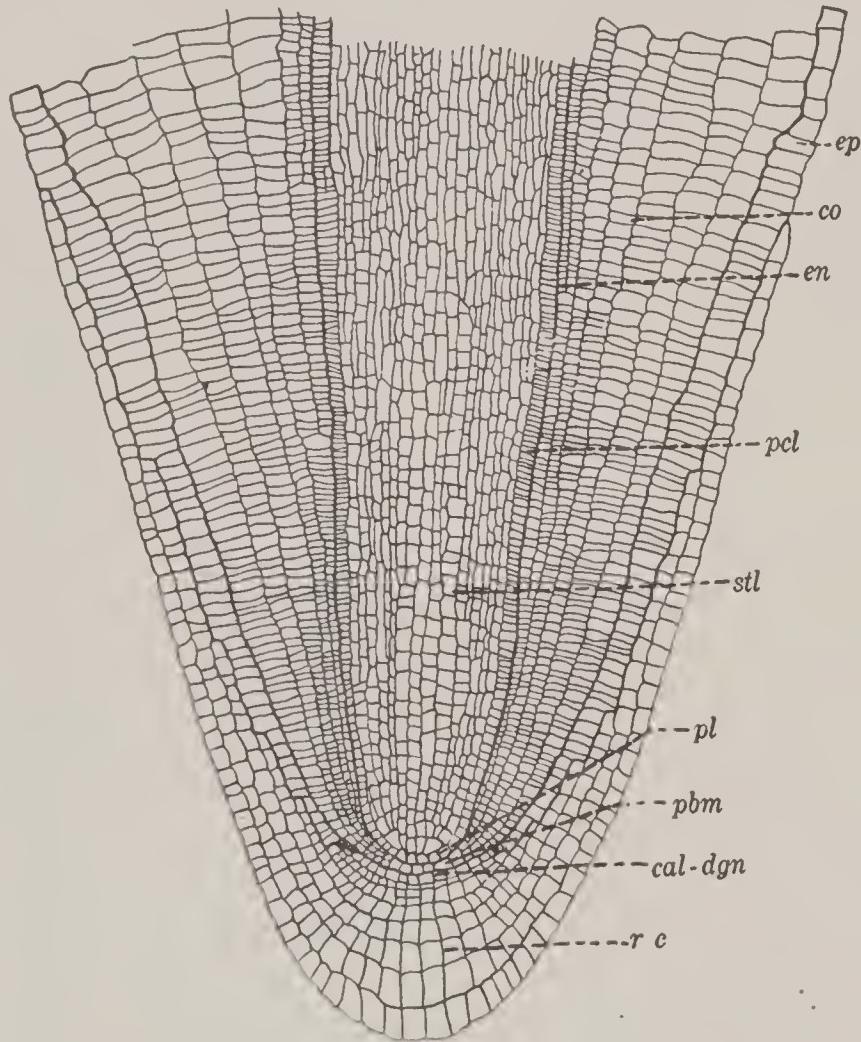


FIG. 146. Median longisection of root apex showing histogens at growing point: *cal-dgn*, calyptrogen-dermatogen; *co*, cortex; *en*, endodermis; *ep*, epidermis; *pbm*, periblem; *pcl*, pericycle; *pl*, plerome; *rc*, root cap; *stl*, stele. (After Grassley.)

final periclinal division of the innermost row of cortical cells which takes place at about the level where the epidermis is no longer enclosed by the root cap. The plerome produces the cells of the stele which are at first slightly and later greatly elongated. The median cell of the plerome gives rise to the metaxylem elements; while the protoxylem, phloem, fundamental parenchyma, and pericyclic cells are derived from the lateral ones.

As the maturation of the cells derived from the three histogens

proceeds, the diarch, radial protostele, cortex and epidermis may be clearly distinguished approximately one millimeter from the tip of the root. At this level, the epidermal cells are nearly isodiametric and the cortical parenchyma consists of thin-walled cells which have formed many intercellular spaces. The cells of the endodermis are small and compactly arranged, with no intercellular spaces. Before there is any differentiation of the secondary cell walls of the primary xylem, the centrally located metaxylem vessels can be distinguished by their larger caliber, as well as the elongated parenchymatous elements of the protophloem.

The protoxylem develops centripetally and the first elements differentiate from the procambial cells abutting the pericycle as spiral vessels. The metaxylem vessels are scalariform or reticulate, some of the latter approximating the pitted type. The primary xylem and phloem are separated by a zone of parenchymatous cells from which the cambium is later differentiated. The pericycle is at first a uniseriate layer; but very early in ontogeny becomes multi-layered as a result of periclinal divisions. At this stage, the epidermal cells elongate slightly in their axial dimension, the cortical cells enlarge in all three dimensions, keeping pace with the increase in the size of the stele, and the cells of the endodermis develop well-defined Caspary strips on their radial and end walls.

LATERAL Roots. — The initiation of lateral roots is coincident with the maturation of the large, reticulate, metaxylem elements. Their point of origin is definitely related to the diarch structure of the stele since the root primordia arise in the pericyclic region outside the protoxylem points or in some cases slightly tangent to them. This results in the formation of two rows of lateral roots which appear to arise from longitudinal furrows. These are not present at the initiation of lateral root formation, but result from the less rapid development of the tissues in the plane of the secondary roots. The number of secondary roots may be large, depending upon cultural conditions, but they are limited for the most part to the lower portion of the fleshy tap root, very few being formed in the upper hypocotyl. The structure of the lateral root resembles that of the non-fleshy portion of the primary root.

THE HYPOCOTYL. — Except for a zone 2 or 3 mm. in length, the hypocotyl elongates rapidly in the young seedling owing to continued division and enlargement of the cells. There is little struc-

tural difference between the middle and lower hypocotyl, but the basal portion of the latter resembles the primary root except that the epidermal cells produce no root hairs and their outer walls are slightly cutinized. In addition, two or three layers of subepidermal cortical cells may exhibit some cutinization. The point at which these differences appear has been termed the collet.

VASCULAR TRANSITION. — The first transitional changes occur in the lower hypocotyl where the groups of phloem cells are extended circumferentially to form two crescent-shaped sectors. In the middle hypocotyl, there is a separation of each phloem sector into two groups. Coincident with this change in the position of the primary phloem, the metaxylem is differentiated in a lateral direction in relation to the spiral protoxylem vessels rather than in a centripetal one. Thus two broad wedges of scalariform and reticulate metaxylem elements are formed extending from each protoxylem strand, while the central region of the axis consists of undifferentiated pith parenchyma. (Fig. 147, *B, C.*)

Grassley (7) has described the hypocotyledonary transition in detail.

"The change from a root structure to stem structure occurs in the upper hypocotyl. The first indication of such a change is in the formation of a central pith which separates the differentiating primary xylem into two distinct units. The primary phloem groups at this level form two broad arcs in the inter-cotyledonary plane, and at a slightly higher level these divide into two tangentially oriented groups, one on either side of the bifurcated xylem units. Each xylem unit and the two groups of phloem adjacent to it constitute a cotyledonary trace. (Fig. 148, *C, D.*)

"Procambial strands of the foliar traces of the first two foliage leaves appear in the intercotyledonary plane between the vascular elements of the cotyledonary traces. (Fig. 147, *C, L-1, L-2.*) The vascular tissue of the hypocotyl at this level forms a siphonostele made up of two cotyledonary traces and two leaf traces of the foliage leaves. Just above this point, lateral veins are diverged from either side of the cotyledonary traces. These with a second set of branches which diverge from the midrib of the cotyledonary petioles at a higher level form the main veins of the cotyledons.

"The branches of the cotyledonary traces which diverge outwardly from the midrib above the base of the cotyledons are endarch bundles. Complete transition to the endarch collateral arrangement does not occur in the upper hypocotyl. The arrangement of the vascular tissues at the base of the cotyledonary petioles is the same as in the upper hypocotyl. (Fig. 147, *D.*) At a higher level in the petiole, the protoxylem

elements of the midrib are oriented more in the adaxial direction and the metaxylem differentiates more in the abaxial direction so that the endarch relationship is attained."

THE COTYLEDONS. — There are five endarch collateral bundles in the elongated petiole which enter the notched obovate blade. The

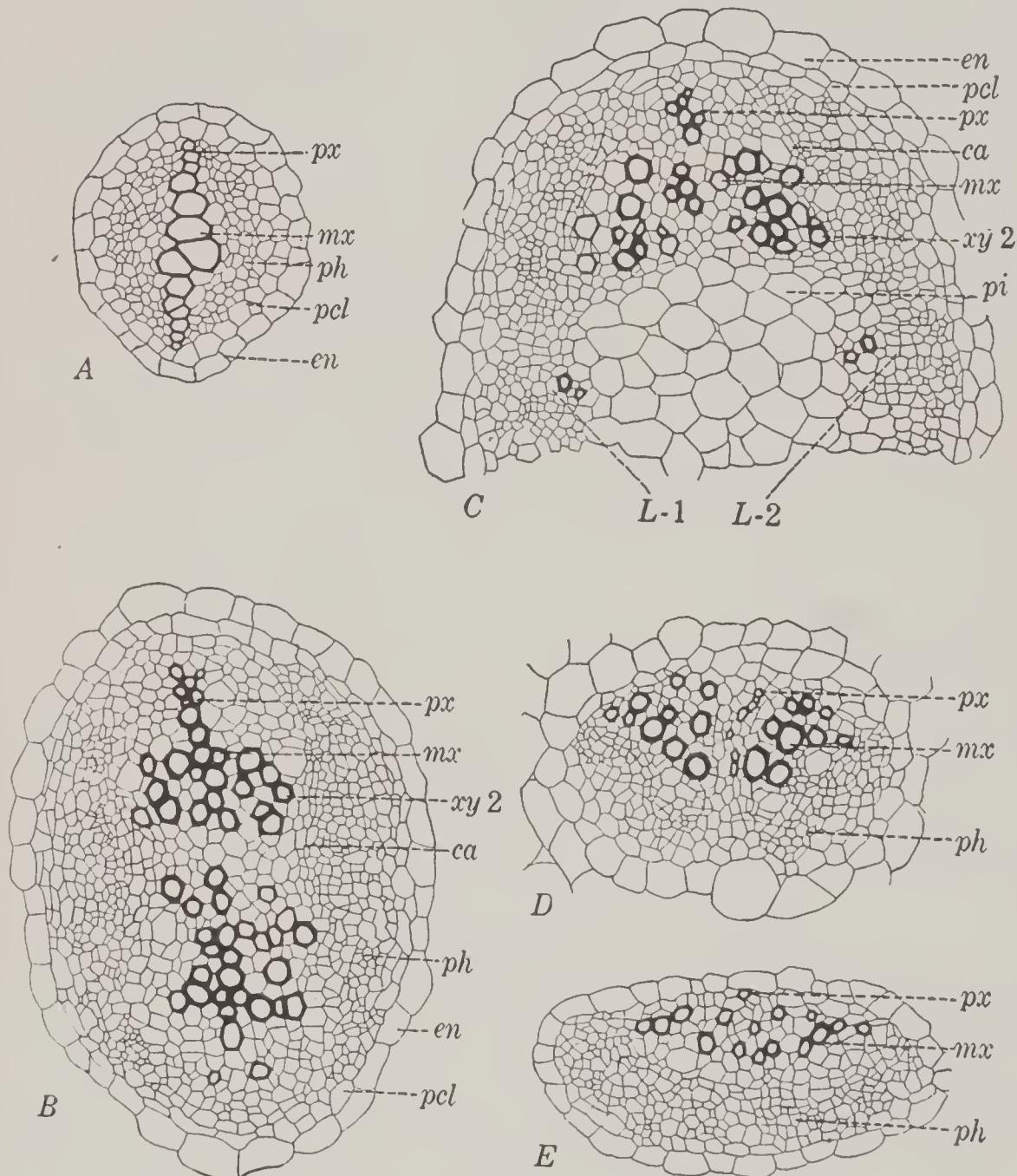


FIG. 147. Stages in vascular transition: *A*, transection of stelar portion of primary root; *B*, lower hypocotyl, transection of stele showing lateral orientation of metaxylem, and central parenchyma; *C*, upper hypocotyl, transection of portion of stele showing laterally oriented metaxylem, and traces of first and second foliage leaves; *D*, transection of cotyledonary petiole, showing lateral placement of metaxylem; *E*, higher in cotyledonary petiole, showing lateral placement of metaxylem: *ca*, cambium; *en*, endodermis; *L-1* and *L-2*, leaf traces of first and second foliage leaves; *mx*, metaxylem; *pcl*, pericycle; *ph*, phloem; *pi*, pith; *px*, protoxylem; *xy 2*, secondary xylem. (After Grassley.)

mesophyll consists of three to five rows of palisade cells and the spongy parenchyma occupies a zone as thick as the palisade region, being made up of cells that are compactly arranged, so that the intercellular spaces are very small. Stomata are more abundant on the lower than on the upper surface. (Fig. 154, F.)

SECONDARY THICKENING OF PRIMARY ROOT AND HYPOCOTYL. — Secondary thickening begins early in ontogeny; and approximately at the time that the first foliage leaf appears, the hypocotyl and

upper portion of the root begin to enlarge. This increase results from the growth of the stelar portion of the axis, since the cortical and epidermal cells do not divide or enlarge to any great extent after the primary tissues of the stele are completely differentiated. As a result, there is a rupturing of the epidermis and cortex, forming two longitudinal splits that arise in the transitional region of the hypocotyl below the cotyledonary plate and extend down toward the root. The splits so formed lie in a vertical plane which is median

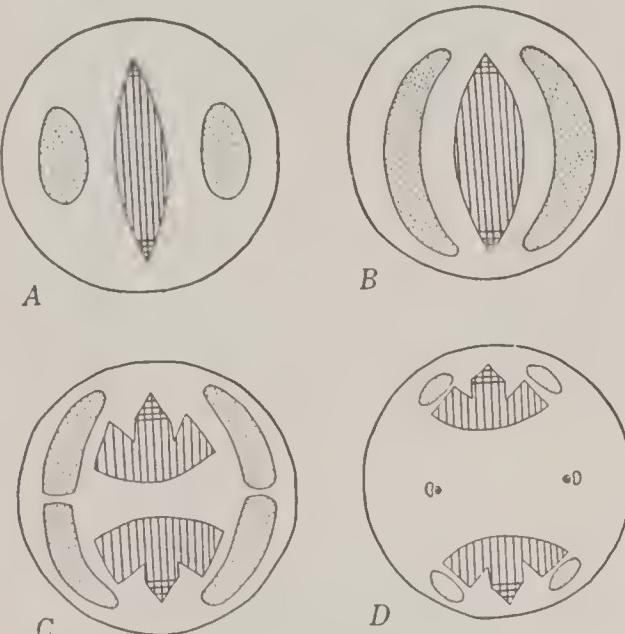


FIG. 148. A-D, diagrams showing stages in vascular transition: A, at root level; B, lower hypocotyl; C, middle hypocotyl; D, upper hypocotyl. Stippled portions represent phloem; cross-hatched areas, protoxylem; lined areas, metaxylem. (After Grassley.)

between the two cotyledons; and as enlargement continues, these are extended nearly to the cotyledonary node. Two flap-like segments of partially split off cortical tissue may remain in the plane of the cotyledons until the fleshy axis has reached its maximum size. (Fig. 150.)

Except for the green upper portion, there is little axial elongation of the hypocotyl after the maturation of the primary tissues unless there are unfavorable environmental conditions, such as dryness or light deficiency, which delay the initiation of secondary thickening. In such cases, the entire hypocotyl elongates considerably and there may be little or no secondary thickening. Temperature may also have a pronounced effect upon the development of the hypocotyl, and Plitt (13) found that under short day conditions

there were fewer thickened hypocotyls at 25° C. than under long day, while at 15.5° C. the thickening of the axis was well developed in both cases.

At the time of initiation of secondary thickening, the differentiation of the primary xylem is practically complete. (Fig. 149.) The cambium arises in the fundamental parenchyma lying between the metaxylem and the primary phloem. The activity begins in this zone at a mid-point on the inner face of the primary phloem; and, as growth continues, there is a lateral extension of

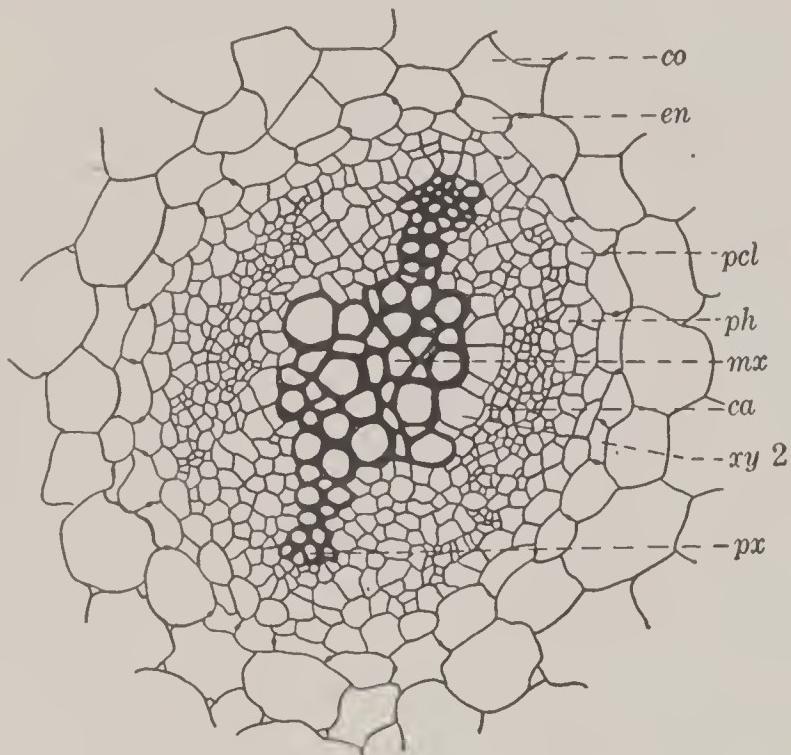


FIG. 149. Transection of stelar portion of root at time when secondary thickening has been initiated: *ca*, cambium; *co*, cortex; *en*, endodermis; *mx*, metaxylem; *pcl*, pericycle; *ph*, phloem; *px*, protoxylem; *xy 2*, secondary xylem, still immature.

the cambium which finally involves the pericyclic parenchyma abutting the protoxylem points. The occurrence of the first cambial activity in a plane at right angles to that of the cotyledons accounts for the splitting of the cortex and epidermis described above. The secondary phloem consists of sieve tubes, companion cells and some parenchyma while the secondary xylem is made up of large reticulate vessels surrounded by parenchyma.

As the root and hypocotyl thicken, they tend to become somewhat oval in transection, but subsequent secondary and tertiary growth may result in an axis that is sub-terete. In the sectors of the cambial ring which arise by an activation of the pericyclic cells outside the protoxylem points, no vascular elements are

differentiated and two broad parenchymatous rays are formed which may be regarded as either pericyclic or secondary xylem rays. (Fig. 152, C.)

A periderm arises in the persistent multi-layered pericycle forming the outer surface of the radish. (Fig. 152, E.) The phellogen

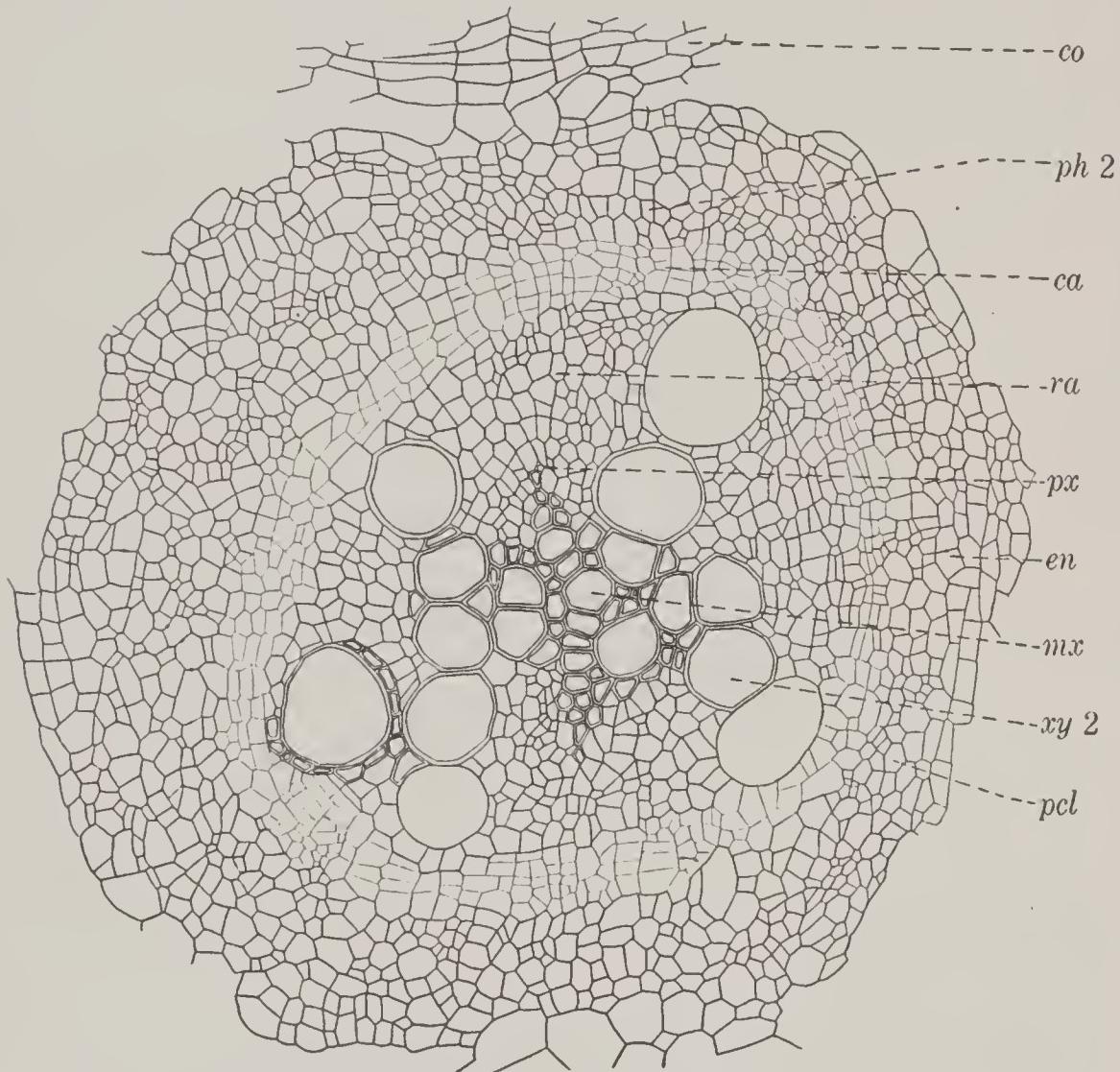


FIG. 150. Transection of young root axis in which secondary thickening has caused splitting of cortical zone: *ca*, cambium; *co*, remains of ruptured cortex which forms persistent flap in cotyledonary plane; *en*, endodermis; *mx*, metaxylem; *pcl*, pericycle; *ph 2*, secondary phloem; *px*, protoxylem; *ra*, ray; *xy 2*, secondary xylem.

which produces it is not continuous but consists of plates of tissue that are more or less overlapping. As the axis increases in size, there are frequently flaky plates of cork cells which are shed and replaced by new phellem. In red radishes the pericyclic cells contain anthocyanin.

The secondary xylem vessels are arranged in approximate radial rows separated by parenchyma, but they may be somewhat dis-

placed tangentially and widely separated from one another radially by the continued growth and division of the parenchyma. (Fig. 151.) The limited development of lignified vascular elements and the differentiation of abundant thin-walled parenchyma from the cambial derivatives accounts for the succulence of the edible root-hypocotyledonary axis. The vessels are relatively large with walls that are reticulately thickened or pitted. Reticulate thickening is more common where the vessels adjoin parenchymatous cells, and pits commonly occur between adjacent vessels. The vessel segments vary in length, ranging from two to five or six times as long as broad; and the end walls, which are resorbed as the vessel develops, are transverse or slightly oblique. There is great variation in the width of the vessel, some being much narrower than others. Each vessel is surrounded by parenchyma consisting of rows of thin-walled, elongated, prismatic cells which have pointed or transverse end walls. There are also radially arranged, isodiametric, parenchymatous cells which are produced in progressively larger numbers as the diameter of the axis increases. The vessels immediately centrad to the cambial ring in a nearly mature radish are widely separated tangentially by rays of parenchyma.

Further activity of the xylem parenchyma results in the development of crescentic or circular zones of secondary cambium which give rise to tertiary xylem and phloem elements. (Fig. 151.) In these regions, vascular strands may be differentiated having a central phloem, a type frequently found in the Cruciferae. Tertiary thickening may be extensive, and this activity, together with a general division of the secondary xylem parenchyma, supplements the function of the primary cambium, and with the latter accounts for the fleshiness of the axis. (Fig. 152, E.) The amount of secondary phloem produced is relatively small as compared with the xylem, and the pericyclic zone is narrow. The vascular strands which are differentiated in interrupted radial rows are not vertical but form a reticulate system by branching and anastomosing.

The secondary and tertiary thickening of the hypocotyl is identical to that described for the root, except that there is a central pith in the upper transitional portion of the former. The development of secondary xylem proceeds as in the root and two broad sectors develop separated by wedge-shaped parenchymatous rays outside the protoxylem points. The cortex is shed as in the root region, but this occurs later in ontogeny.

Minin (11) and Golinska (6) suggest that the enlargement of the axis does not always occur at the same level, and the former main-

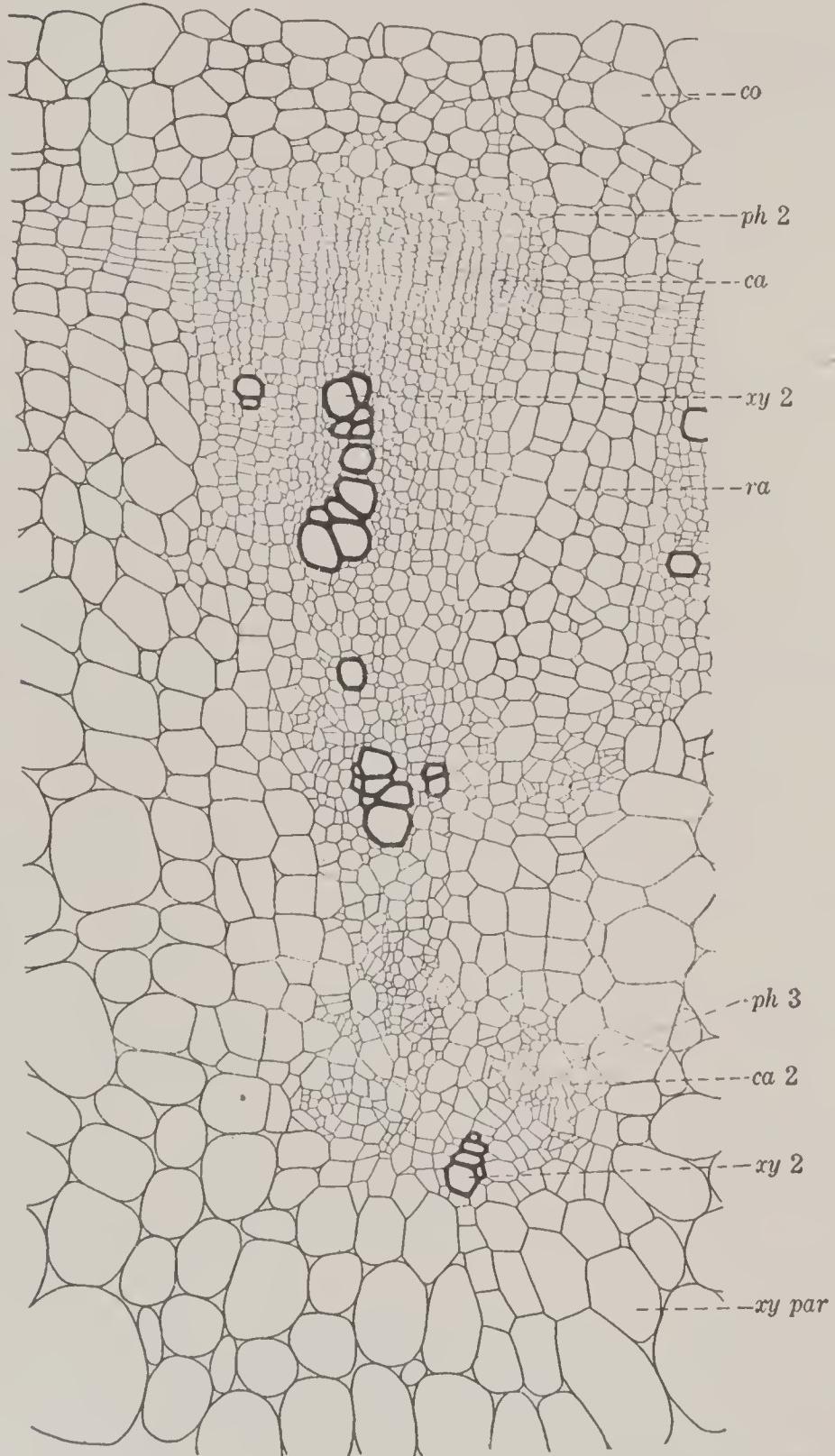


FIG. 151. Transection of sector of fleshy portion of hypocotyl showing secondary and tertiary thickening. Secondary cambium arising in secondary xylem parenchyma have already produced tertiary phloem: *ca*, cambium; *ca* 2, secondary cambium; *co*, cortex; *ph* 2, secondary phloem; *ph* 3, tertiary phloem; *ra*, ray; *xy* 2, secondary xylem vessels; *xy par*, secondary xylem parenchyma.

tained that the root and hypocotyl can replace each other in constructive function, "konstruktiver Funktion." He experimented with a Red Globe type, cutting away two-thirds of the hypocotyl of the young seedling. The remaining portion developed roots and produced a normal fleshy axis. Golinska repeated the experi-

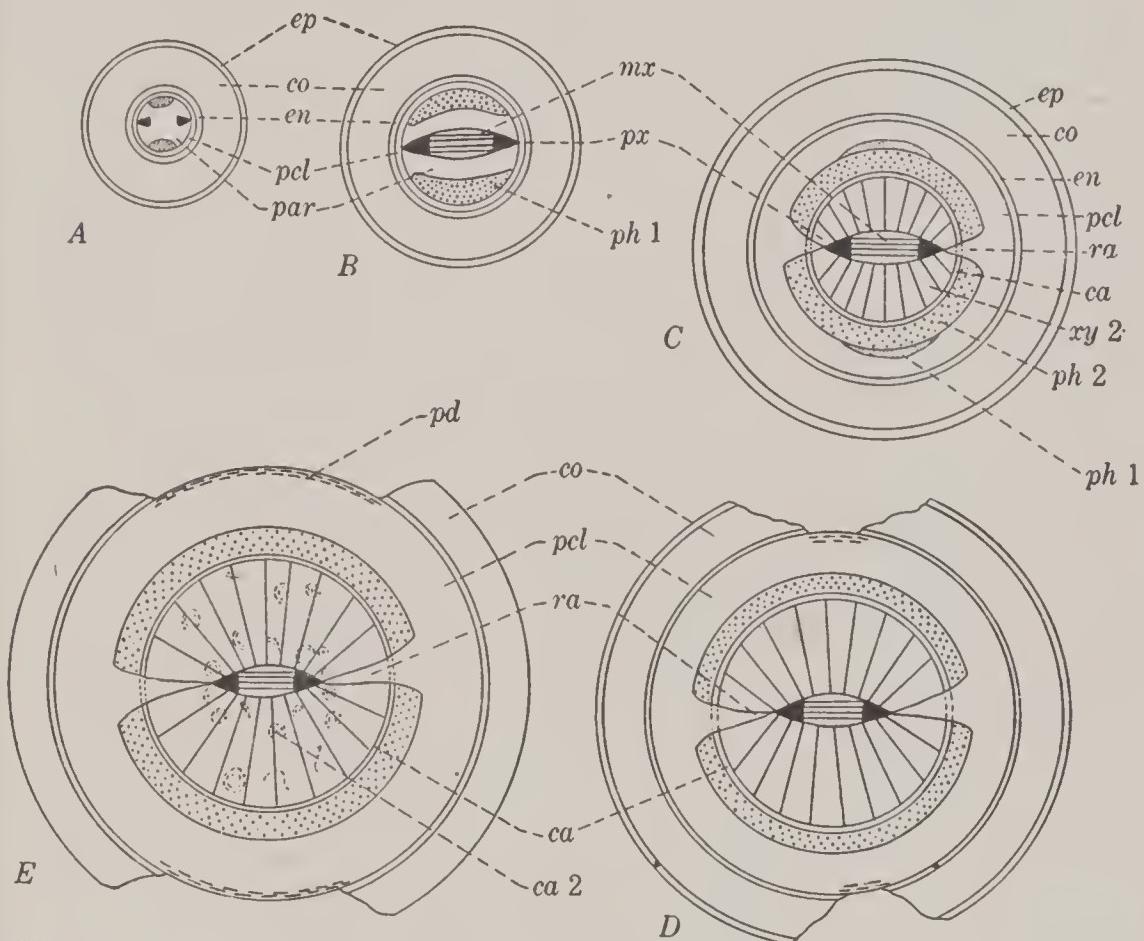


FIG. 152. Diagrams illustrating progressive stages in secondary and tertiary thickening of fleshy axis of *Raphanus*. *A*, root before primary xylem is completely differentiated; *B*, same, with primary xylem strand differentiated; *C*, secondary thickening and development of two broad rays outside protoxylem points (two sectors of crushed primary phloem are also indicated); *D*, secondary thickening has resulted in splitting of cortical zone in a vertical plane at right angles to primary xylem strand and cotyledons; *E*, further splitting of secondary xylem parenchyma: *ca*, primary cambium; *ca* 2, secondary cambium; *co*, cortex; *en*, endodermis; *ep*, epidermis; *mx*, metaxylem; *par*, parenchyma; *pcl*, pericycle; *pd*, periderm; *ph* 1, primary phloem; *ph* 2, secondary phloem; *px*, protoxylem; *ra*, ray; *xy* 2, secondary xylem.

ments of Minin, using large elongated radishes. He made cuttings at a time when the seedling had developed its cotyledons and a few small foliage leaves. In most of the plants, the upper portion of the hypocotyl and even the epicotyl enlarged while the lower portion remained slender, indicating that the potentialities for secondary thickening exist throughout the axis.

FOOD RESERVES. — There is little stored food in the radish, the bulk of the fleshy axis being water and cellulose. Some reserves are accumulated in the thickened hypocotyl in the form of glucose and there is a small amount of fructose. In certain Chinese types, there may be a considerable amount of starch; but the French, Japanese, and American varieties contain little if any under normal conditions. In this connection, Plitt (13) found that slightly thickened hypocotyls grown at high temperature with a long day contained many small starch grains in the parenchyma.

ANATOMY OF THE MATURE STEM. — The mature stem is sub-terete or somewhat lobed and fluted in transection. The vascular bundles are collateral and form a dissected siphonostele, but adjacent bundles may be connected by a weak interfascicular cambium at maturity. In addition to this, the thickening of the parenchymatous cells surrounding the bundles results in the formation of a practically uninterrupted zone of connective tissue giving the vascular ring the appearance of complete continuity. The bundles vary in size with the larger ones occupying the arcs of the vascular ring centrad to the lobed or ridged portions of the stem. (Fig. 22.)

Both of the tangential walls of the epidermal cells are thicker than the radial and end walls, the outer one being slightly cutinized. The stomata are subtended by small guard cells and are continuous with substomatal cavities in the chlorenchyma. The chlorenchyma consists of a compact subepidermal layer and several adjacent layers of spongy cells which are smaller than the non-chlorophyllose parenchyma centrad to this zone.

The phloem of each collateral bundle is capped by an arc of pericyclic fibers. The sectors of fibers which subtend the larger bundles are more fully developed than those outside the smaller ones; and, together, they form a discontinuous cylinder of mechanical tissue. Adjacent bundles are separated by medullary rays of thin-walled parenchyma but later in ontogeny the walls thicken. In some instances, an interfascicular cambium may form across the ray and produce several radial rows of non-vascular tissue. (Fig. 153.) Except for the connective tissue which forms a thickened sheath around the xylem portion of each collateral bundle, the pith consists of parenchymatous cells; and the stem is commonly hollow at maturity owing to the disintegration of the central cells. The primary xylem consists of annular and spiral elements that are separated from each other by thin-walled parenchyma. The

large, secondary xylem vessels are reticulate or pitted and are surrounded by small thick-walled cells. The secondary phloem is comprised of sieve tubes, companion cells, and parenchyma.

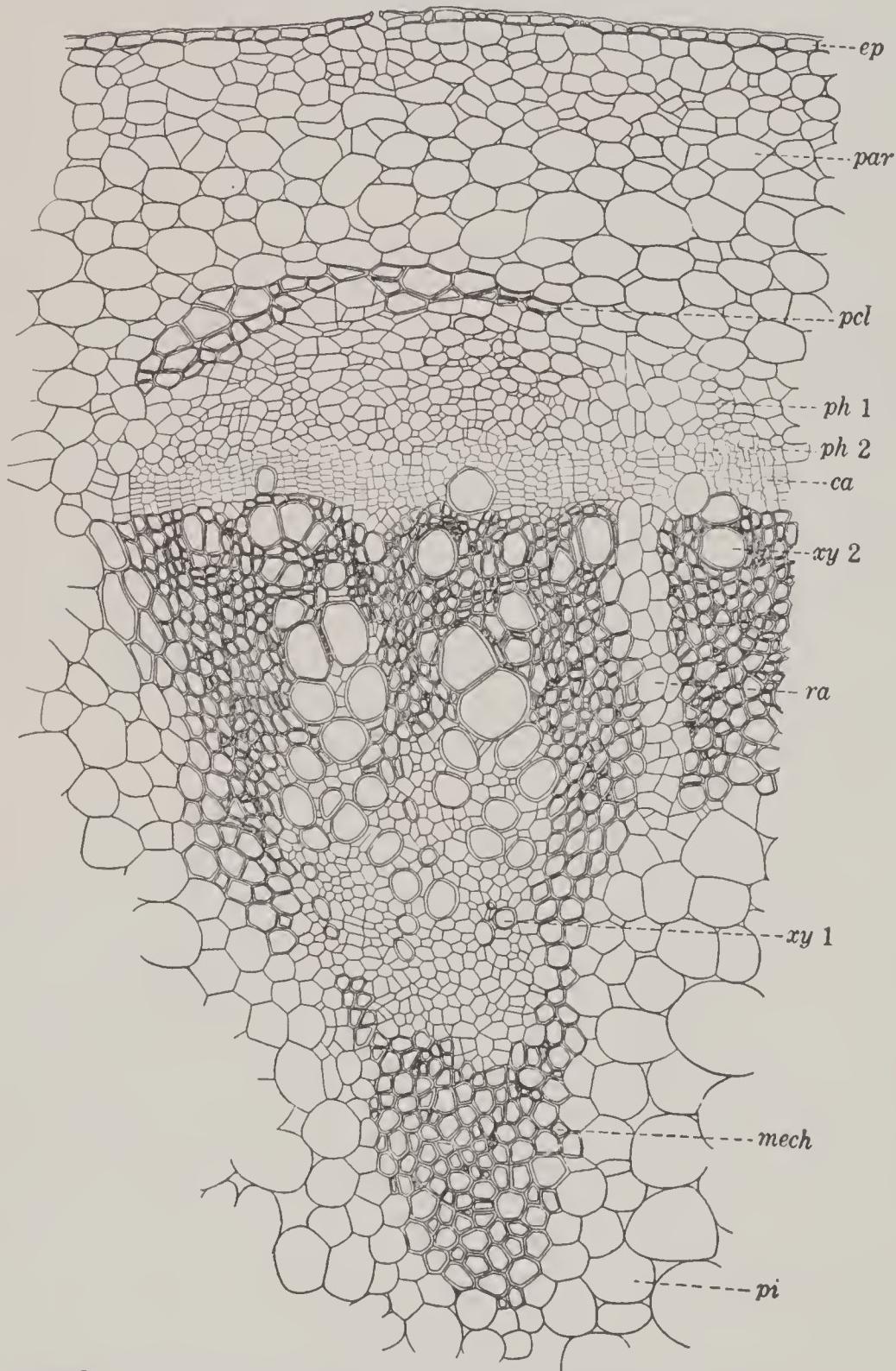


FIG. 153. Sector of old stem in transection showing vascular bundle: *ca*, cambium; *ep*, epidermis; *mech*, mechanical tissue; *par*, cortical parenchyma; *pcl*, pericyclic fibers; *ph 1*, primary phloem; *ph 2*, secondary phloem; *pi*, pith; *ra*, medullary ray; *xy 1*, primary xylem; *xy 2*, secondary xylem.

THE LEAF. — The petiolate basal leaves which form a rosette in the first phase of vegetative development are variously incised and deeply lobed or lyrate pinnatifid. The petiole encircles the stem for about a third of its circumference, and its basal margins, which are winged, continue as a ridge as far as the lobes of the lamina. (Fig. 154, A.) The vascular supply consists of five collateral bundles which occupy positions corresponding to the lobing of the petiole. Each bundle is made up of three to five units which are separated from one another by parenchymatous rays. The bundles are crescent-shaped with the open arc directed toward the adaxial surface of the petiole, and transverse veinlets cross-connect the main ones. There is a well-defined cambium in the principal veins which gives rise to some secondary vascular tissue. The phloem is bounded by a zone of mechanical tissue, comparable to the pericyclic strands in the stem; and the parenchymatous cells adaxial to the bundle and between the rows of the secondary xylem may also be thick-walled.

The subepidermal layers are chlorophyllose and there are chloroplasts in the cells immediately outside the mechanical tissue of the bundles, in the phloem parenchyma, and in the parenchymatous rays separating the radial rows of xylem in each bundle. Anthocyanin may occur in the cells of the epidermal layers, but this condition is a variable one.

The surfaces of the blade are much roughened, and the veins form prominent abaxial ridges. The degree of pubescence is not constant, but commonly there are epidermal hairs sparsely distributed over both surfaces, especially along the veins on the abaxial one. The large, stiff, unicellular hairs extend from a basal group of slightly raised epidermal cells. (Fig. 154, D.) The latter are roughly pentagonal or hexagonal in surface view except over the veins, where they are rectangular and much elongated, with their long axes parallel to the vein. The mesophyll consists of a single-layered palisade region and the spongy parenchyma which is several cells in thickness. The air passages are large and some of the palisade cells may be transversely divided so as to form a partial double layer. (Fig. 154, C.) Chloroplasts occur in all the cells in the mesophyll and the guard cells, but are absent in the tissue surrounding the principal veins. At these points, the parenchymatous cells are compact and there is a sheath of mechanical tissue as in the petiole. The venation is pinnate-reticulate with fre-

quent lateral connections between the main bundles, and the ultimate veinlets end blindly in the mesophyll.

Stomata are more abundant in the lower than the upper epidermis. They are formed by successive divisions of an initial epidermal cell in which anticlinal walls are laid down so that the

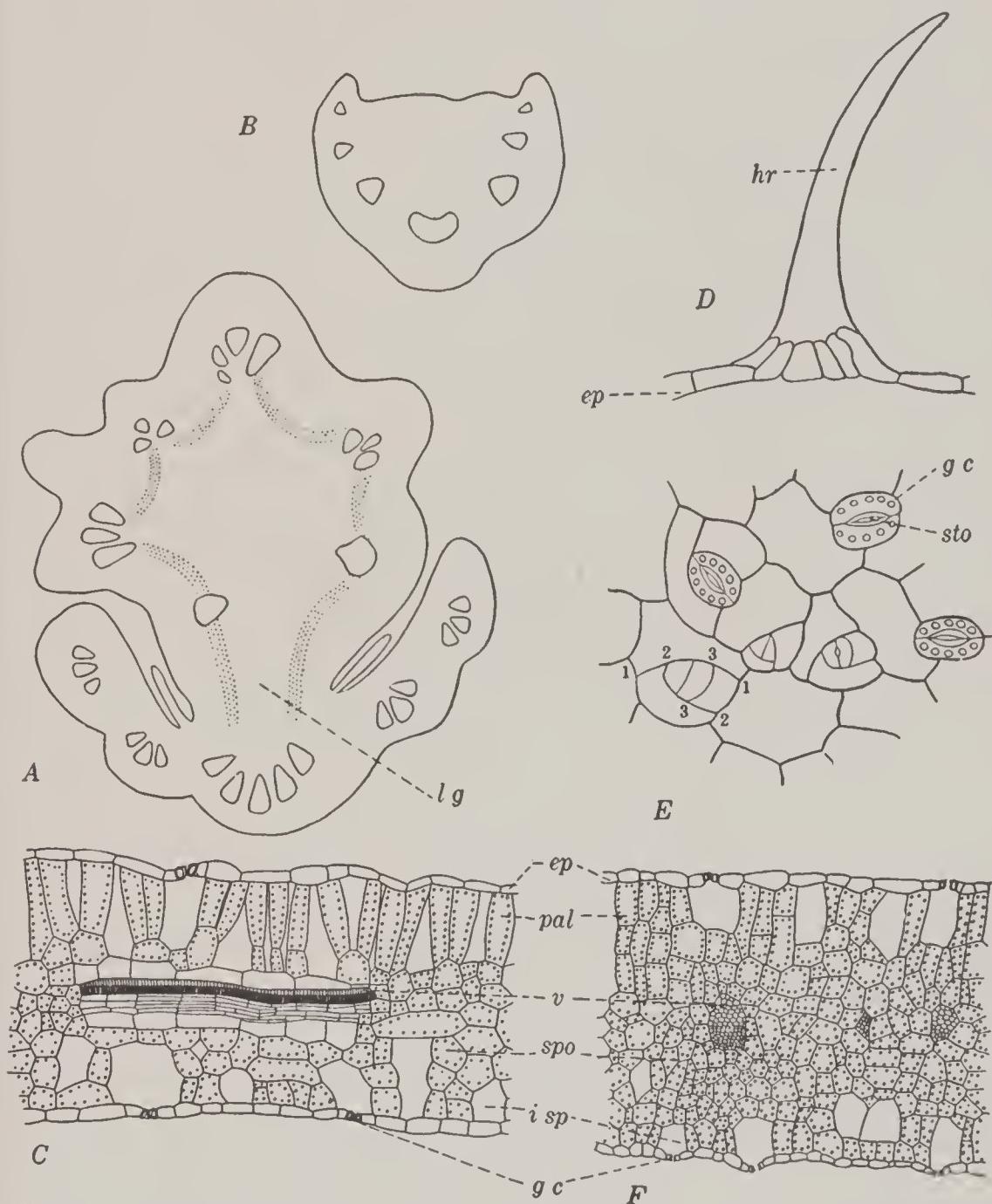


FIG. 154. A, diagrammatic transection of young stem and petiole showing vascular bundles; B, same, of petiole; C, transection of sector of blade; D, epidermal hair with basal cells (much enlarged); E, surface view of epidermis showing ontogeny of stoma: 1-1, 2-2, 3-3 indicate successive anticlinal walls which divide initial cell into mother cell and surrounding accessory cells. A final division of mother cell forms two guard cells; F, transection of sector of lamina of cotyledon: ep, epidermis; gc, guard cell; hr, epidermal hair; i sp, intercellular space; lg, leaf gap; pal, palisade cells; spo, spongy cells; sto, stoma; v, vein.

stomatal mother cell is surrounded by a few subsidiary or accessory cells. A final division of the stomatal mother cell then produces the two guard cells which subtend the stoma. (Fig. 154, E.)

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CHAPTER XI

LEGUMINOSAE

MEDICAGO SATIVA

THE large pea family is widespread and contains a number of species of economic plants, among which are *Pisum sativum* L., *Phaseolus vulgaris* L., *Trifolium pratense* L., *Medicago sativa* L., and many others grown for food or decorative purposes. The clovers and medics are important forage plants, and alfalfa is an outstanding representative of the group. A native of southwestern Asia, where it was used as a forage crop centuries before the Christian era, it has spread successively to Greece, Italy, Spain, Mexico, and South America. According to Bailey (2), it was introduced into New York from Europe as early as 1791, and was cultivated there in limited areas. It was brought into California from Chile in 1854; and to Texas from Mexico in the early part of the nineteenth century. Since introduction, its production has extended over the entire western half of the United States until it is now one of the principal forage crops west of the Mississippi.

There are approximately 55 species of the genus *Medicago*, of which seven are perennial and one biennial or perennial. Although the commonly grown alfalfa is known as *Medicago sativa* L., it seems probable that many of the commercial strains are hybrid forms. It has been suggested by Westgate (34), and by Garver (12), that crossing of *M. sativa* with the yellow-flowered *M. falcata* has occurred, and that this has contributed to the hardiness of northern strains of alfalfa such as Grimm, which is classified as *M. media* by some authorities. Fryer (11) has confirmed this point on the basis of cytological evidence, stating that "Cytological study has shown the chromosomes of *Medicago sativa*, *M. falcata* (32-chromosome form) and *M. media* to be the same in number and very similar morphologically"; and he concludes that "there is therefore no reason, from cytological considerations, to doubt the origin of *M. media* from interspecific hybridization between *M. sativa* and *M. falcata*."

GENERAL MORPHOLOGY

The alfalfa plant is a long-lived perennial, its average length of life being from five to seven years, depending upon environmental conditions. It is known as a deep feeder and grows best in soils of a type in which a deeply penetrating root system can develop. Where this is not possible, there is an increase in the amount of branching and in the lateral spread of the branches formed.

THE ROOT AND SHOOT. — The young plant develops a tap root that penetrates very deeply and rapidly, often reaching depths of five to six feet the first season of growth. (Fig. 155.) Garver (12) estimated the volume of soil occupied by a single three-year-old plant to be 3 feet in diameter and 10 feet in depth. According to Weaver (33), it may penetrate to 10 or 12 feet by the end of the second year; and, ultimately, may extend to depths of 20 feet or more. It develops a few branches in the first inches of surface soil; but these, instead of spreading laterally, penetrate more deeply and finally follow a course parallel to the tap root. Frequently, branches are limited in number and the tap root is always the most important part of the root system.

From the short stout crown stem, numerous erect branches arise which attain a height of 1 to 4 feet. In hardy types, such as Grimm alfalfa, the woody rhizome is branched, and shoots arise from it below or at the soil surface forming a bushy crown. The upper portions are herbaceous; and the slender, aerial stems are much branched, bearing pinnately compound, trifoliate leaves in an alternate phyllotaxy. The leaflets are linear, oblong or obovate-oblong, and toothed toward their apices, with slender, awl-shaped stipules that are adnate to the petiole. (Fig. 157, A.)

THE FLOWER AND FRUIT. — The flowers are borne in short, compact, axillary racemes; and the papilionaceous blossoms are purple or rarely white. (Fig. 156.) In hybrid forms, yellow flowers are occasionally produced; and the sand lucerne, *M. media*, has flowers which vary from yellow to purple. The floral structure and ontogeny are similar to that of the pea in all essential details. (See Chapter XII.)

The calyx tube consists of five undiverged sepals terminated by five lobes or teeth that exceed the length of the tube, and the five petals form a corolla of the papilionaceous type in which the standard is somewhat longer than the two lateral wings, these, in

turn, exceeding the length of the keel. The stamens are diadelphous, nine of them being undiverged with the tenth or uppermost stamen free. The stamens forming the staminal tube are held in a state of tension by two projections of the keel which meet in front

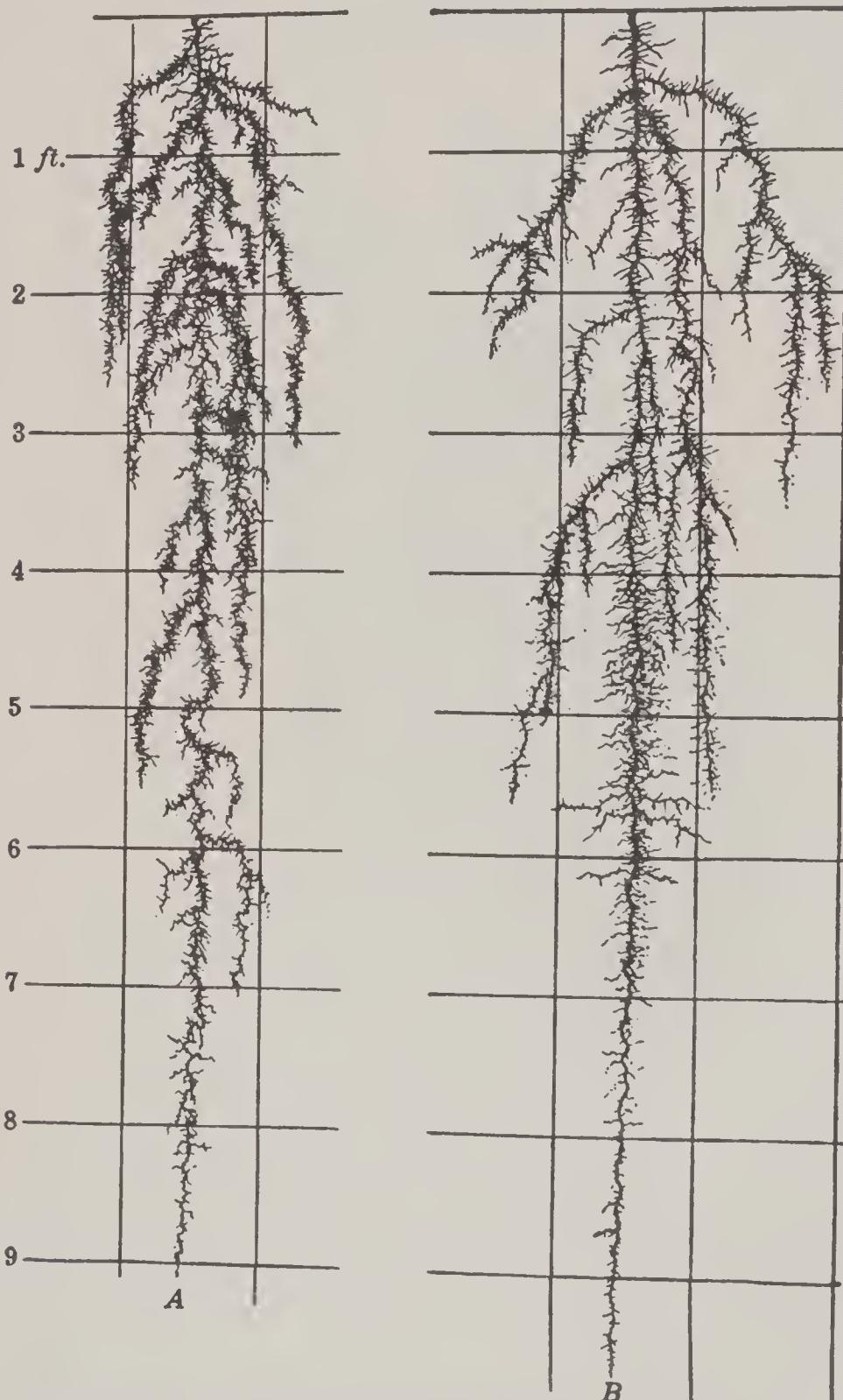


FIG. 155. Root systems of alfalfa in July of second year of growth: A, grown in dry land; B, in irrigated soil. (From Weaver, *Root Development of Field Crops*, McGraw-Hill Book Co.)

of the staminal column; and, in addition, there is a horn-like projection on each wing which fits into the evaginations of the keel. The release of tension in connection with pollination is known as "tripping."

The pistil consists of a single carpel which develops a one-celled, superior ovary, and a smooth, awl-shaped style. (Fig. 157, C.)



FIG. 156. Habit of leaves and inflorescence of Grimm alfalfa. (Photograph by J. Horace McFarland Co.)

In the ovary, 12 to 18 ovules are formed, according to Martin (20); while Cooper (9) reports a smaller range of 10 to 12. From one to six ovules begin to develop after fertilization, the others aborting; and, in heavy seed-producing strains, there is an average of three to four seeds per pod.

The mature fruit is a brown, curved or coiled, slightly pubescent, indehiscent pod which may have two or three spirals. (Fig. 160, A.) The fruit coat consists of three distinct regions. (1) The

epicarp is a single layer of elongated cells, except where they form a rosette around a stoma; and epidermal hairs are frequently formed which tend to break off as the fruit dries, leaving a thickened scar. (2) In the mesocarp, the two important cellular elements are the very thin-walled crystal cells, each of which contains a single crystal; and the fibers which have thick pitted walls and blunt ends. (3) The endocarp consists of a single layer of epidermal cells in which there are no stomata.

POLLINATION. — The variation in the amount of seed produced by a given strain of alfalfa has resulted in many investigations of pollination; and this, in turn, has focused attention on the mechanism of the process. When tripping occurs, due to any of the agencies noted below, the staminal column is released and snaps forward until it strikes the standard with considerable force. This must be sufficient, according to Armstrong and White (1), to rupture the cuticular membrane which constitutes the limiting outer surface of the stigma. The presence of such a limiting membrane was demonstrated by Jost (16) in *Lupinus* and *Cytisus*. Tripping of the stamens may be due to insect visitation; to "automatic tripping" in which some other factor, possibly climatic, may release the tension; or it may be artificially induced by various agencies. Piper and coworkers (25) state that "Atmospheric or climatic conditions greatly affect automatic tripping, so that it is not improbable that this factor alone accounts for a great variation in seed production during different seasons." Carlson and Stewart (7) determined that "artificial tripping resulted in an increase of approximately 140 per cent in the percentage of flowers forming buds as compared with natural development"; and, also, that alfalfa may "be expected to seed best under desert or

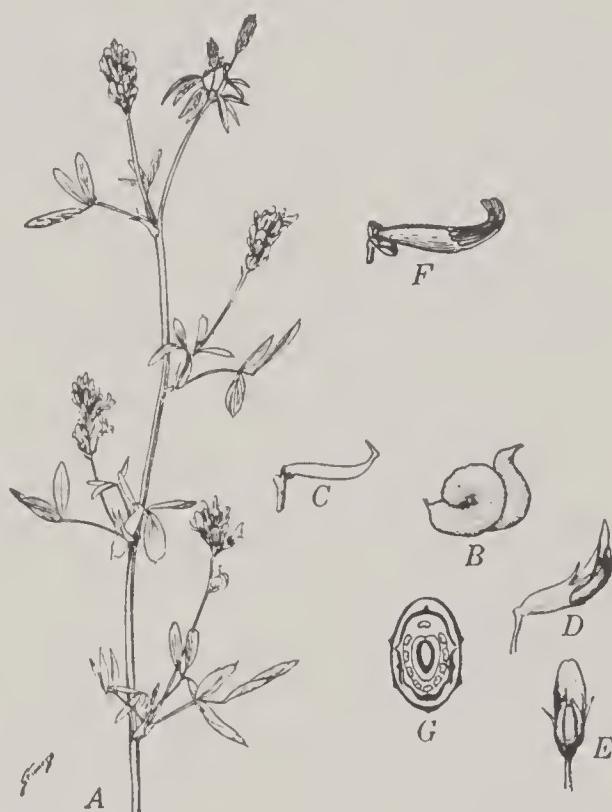


FIG. 157. *A*, habit of inflorescence; *B*, fruit; *C*, carpel with other floral parts removed; *D* and *E*, flower, lateral and face views; *F*, stamens with perianth removed; *G*, floral diagram.

semi-desert conditions, where warm or hot days, cool nights, and a relatively dry air both night and day generally are encountered."

Although it is believed by many investigators that tripping is essential to effective pollination, Brink and Cooper (4) point out that "Under greenhouse conditions in the winter, tripping is practically indispensable to seed setting, but in the field many pods may arise from untripped flowers." Carlson (5) noted in Utah that only about 8 per cent of the flowers were tripped, while 24 per cent set pods; and the semi-arid climate is undoubtedly an important factor in the production of seed in that region. Factors which may tend to decrease the amount of seed produced are variations in the behavior of the stigmatic membrane as a block to effective pollination; abortion of a relatively high percentage of the pollen; and, less frequently, abnormal positional relationships between the stigma and the anthers. An additional factor has been suggested by Martin (20), who attributes blasting of the seed, in some cases, to an arrested development of the embryo, due to the inability of the plant to furnish proper water and food supply; as well as to pathological conditions to which the seed is more susceptible under drought conditions.

MICROSPOROGENESIS. — In the development of the anther, there is an early differentiation of a hypodermal column of archesporial cells one or two layers in thickness. These in turn produce the primary parietal cells and the primary sporogenous tissue by the formation of periclinal walls. The parietal cells again divide periclinally and the outermost layer redivides, so that the anther wall consists of an epidermal layer, two middle layers, and the tapetum. The primary sporogenous cells divide several times to form a column of microspore mother cells. According to Reeves (26), the tapetum differentiates rather slowly and its cells remain uninucleate, while the outer parietal cells become elongated radially and form an endothecium. Later the tapetum and inner layer of parietal tissue disintegrate and their contents are absorbed by the developing microspores; so that, at anthesis, the walls of the locules consist of only the epidermis and endothecium. Following reduction division and wall formation, which occurs by furrowing rather than by the formation of cell plates, the microspores increase in size until they are several times their original diameter. The wall of the slightly three-lobed mature pollen grain consists of an intine and exine layer with three germ pores,

and, prior to dehiscence, the nucleus divides to form two daughter nuclei of unequal size.

Dehiscence of the anthers occurs in the bud stage and the liberated pollen is confined to the keel, closely packed around and directly on the stigma. This method of pollen release leads to self-fertilization in most instances, but there is some cross-pollination. It has been noted that pollen frequently occurs on the standards of untripped flowers in the field, and such grains, which have been transmitted by insects or other agencies, provide an opportunity for cross-fertilization. It has been demonstrated further that cross-fertilization greatly enhances the production of seed, and Carlson (6) reports "that 27 per cent of alfalfa flowers allowed to develop naturally formed seed pods, while 44 per cent of those tripped artificially and 54 per cent of those artificially cross-pollinated formed seed pods."

THE DEVELOPMENT OF THE OVULE AND MEGASPOROGENESIS. — The ovules arise from parietal placentae in two rows which are so crowded that transections of the carpel may show two ovules apparently side by side, but as the carpel lengthens rapidly, they become separated and appear to be in one row. The young ovule is erect, beginning to curve at about the time that it comes in contact with the dorsal wall of the carpel. Reeves (27) observed that the curvature is usually toward the basal portion of the ovary; although, occasionally, one of the ovules at the stylar end may curve toward its apex. (Fig. 158, A.) At maturity, the ovule is campylotropous with the micropyle resting against the funiculus. Two integuments develop, each of which is two cell layers in thickness, except near the micropyle where the outer integument is considerably thicker. In the development of the ovule, the inner integument arises first, but the outer one grows more rapidly and soon encloses it. Since the inner integument does not usually completely surround the nucellus, a considerable part of the nucellus adjacent to the micropyle is covered only by the outer integument. (Fig. 158, B and C.) As the ovary develops, the carpel itself becomes coiled, the curvature being greater at its apical end.

The number of archesporial cells may vary. Martin (19) observed a multiple archesporium from which primary parietal and primary sporogenous cells are derived; and both Reeves (27) and Cooper (9) have noted that there are usually two or three primary

sporogenous cells, which are commonly arranged side by side, but may occur in a linear row. These cells function directly as megasporangium mother cells producing tetrads of megaspores; and, frequently, two or three tetrads are formed in a single ovule. In most instances, only a single chalazal megasporangium of one of the tetrads develops to form a mature megagametophyte; but Cooper reports that an ovule may contain two well-developed gametophytes. The megagametophyte reaches the eight-nucleate stage as a result of three equational nuclear divisions, and cell plates are formed in

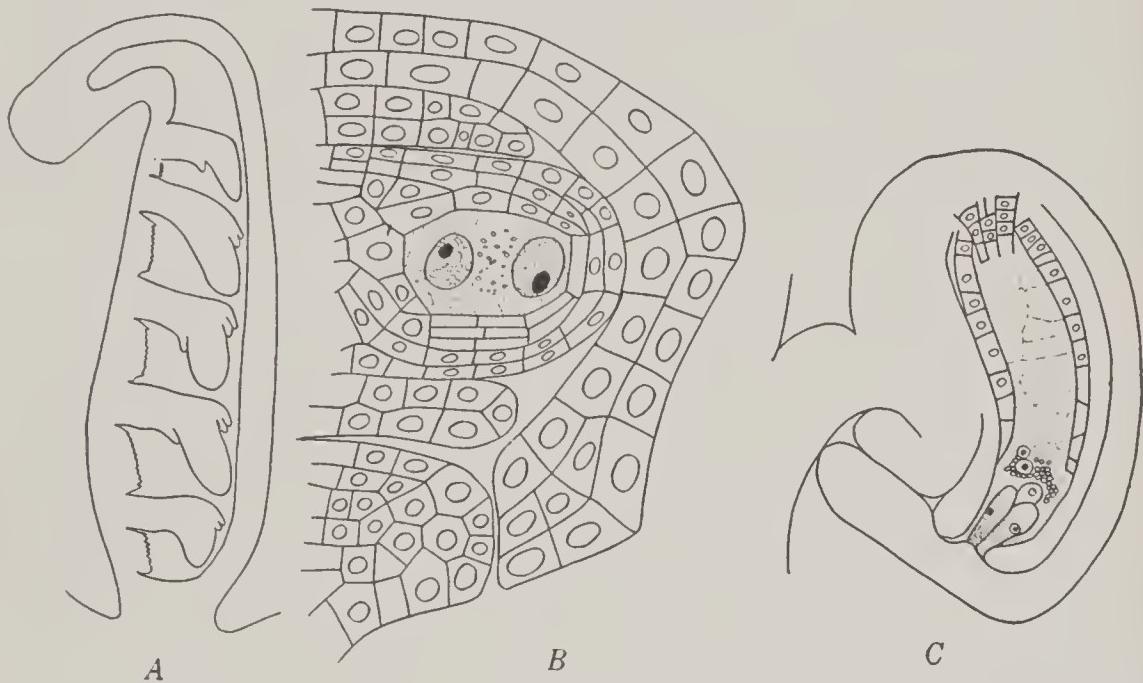


FIG. 158. *A*, longisection of young carpel showing initial stages in curvature of campylotropous ovules; one row of ovules has been removed; *B*, longisection of portion of an ovule showing two-nucleate megagametophyte and two integuments, the outer one completely enclosing nucellus; *C*, longisection of campylotropous ovule showing mature megagametophyte ready for fertilization. (Redrawn after Reeves.)

such a way that three nuclei at each end of the embryo sac are enclosed by walls while the fourth nucleus of each group remains in the central region. In this manner, a seven-celled gametophyte is developed with a megagamete and two synergids at the micropylar end, three antipodals at the chalazal end, and an elongated endosperm mother cell in the central region.

FERTILIZATION AND EMBRYOGENY. — Fertilization occurs approximately 24 hours after pollination, one microgamete uniting with the megagamete while the other fuses with the two polar nuclei to form the endosperm nucleus. The zygote divides transversely to form a two-celled proembryo, and further transverse divisions of the apical cell result in the formation of a proembryo consisting

of a linear row of six cells. (Fig. 159, A, B.) The embryo is developed from the apical cell of the six-celled proembryo, while the remaining cells produce the suspensor.

The first division of the apical cell to form the embryo is, in most instances, parallel to the long axis of the proembryo; and two additional divisions, one vertical and the other transverse, result in the formation of an eight-celled embryo. (Fig. 159, C, D.)

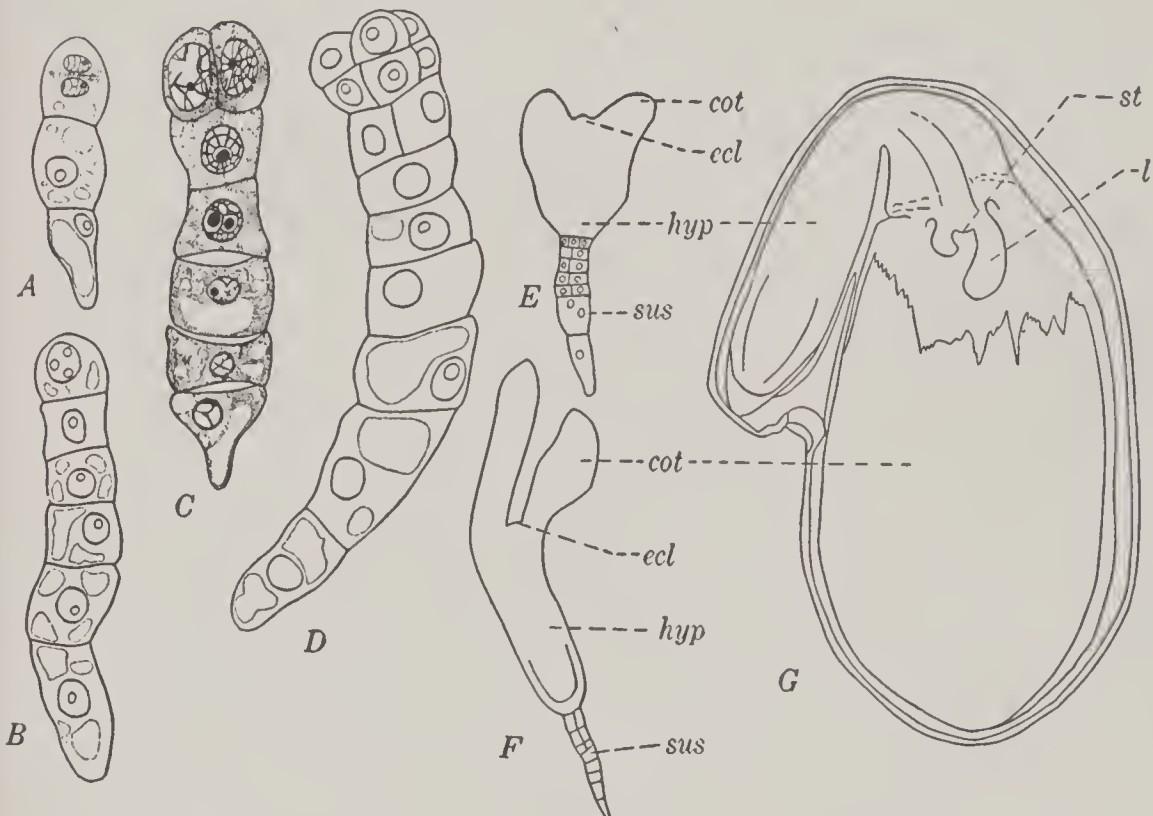


FIG. 159. Stages in embryogeny: A, formation of four-celled proembryo; B, six-celled proembryo; C, two-celled embryo with five-celled suspensor; D, eight-celled embryo with eight-celled suspensor; E, initial differentiation of cotyledons, epicotyl, and hypocotyl with suspensor at stage of greatest development; F, initiation of curvature of embryo in region of epicotyl, the suspensor is disintegrating; G, mature embryo with portion of upper cotyledon removed to show stem tip and leaf primordia: cot, cotyledon; ecl, epicotyl; hyp, hypocotyl; l, leaf; st, stem tip; sus, suspensor. (Redrawn and adapted from Cooper, *Jour. Agr. Res.*)

Subsequent periclinal divisions cut off the dermatogen layer, and continued growth results in the formation of an embryo which is at first spherical and later elongates and broadens at its apex. In the development of the hypocotyl and cotyledons, the former elongates, and this is followed by a curvature of the embryo so that the hypocotyl and cotyledons lie approximately parallel at maturity. (Fig. 159, E, F, G.) There is an early differentiation of the provascular strands, and the advanced condition of the mature embryo is evidenced by the presence of the foliage leaves.

ANATOMY

THE SEED. — The seeds are somewhat kidney-shaped, 2 to 3 mm. in length, about twice as long as broad, and the seed coat is relatively smooth, varying from a dull yellow, sometimes tinged with green, to a reddish brown. (Fig. 160, B.) Its structure, which has been investigated by Pammel (24), Winton (37), and Lute (18), appears to have a significant relation to the problem of germination. The outermost layer of the coat consists of a row of palisade

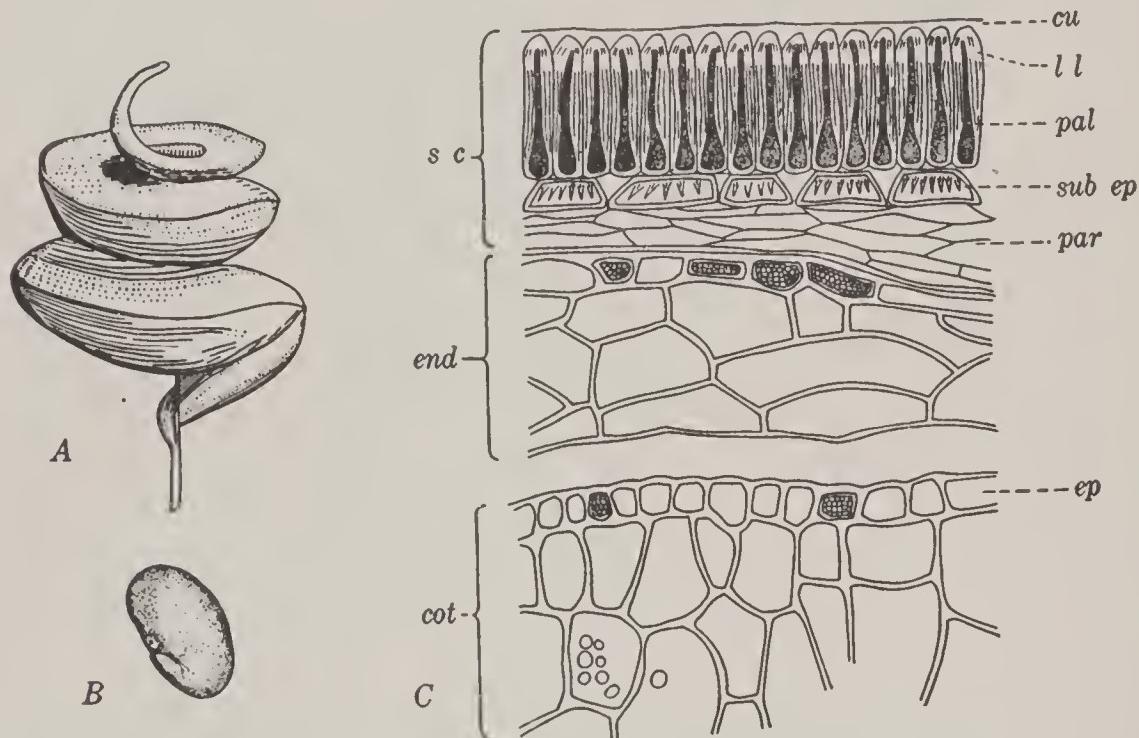


FIG. 160. A, fruit; B, seed; C, transection of portion of seed coat and cotyledon: *cot*, cotyledon; *cu*, cuticle; *end*, endosperm; *ep*, epidermis of cotyledon; *ll*, the light line; *pal*, palisade cells; *par*, parenchyma; *sc*, seed coat; *sub ep*, sub-epidermal layer of "hour-glass" cells. (A and C redrawn after Winton.)

cells, called Malpighian cells by Pammel, which are from 35 to 42 μ high and 8 to 10 μ broad. Their outer ends are rounded, and the exposed surfaces are covered by a thin cuticle which forms a continuous layer of unequal thickness and extends between the conical projections of the palisade cells. (Fig. 160, C.) The "light line" is situated below the cuticle at the upper limits of the palisade layer, and can be readily observed in transections of the seed coat. The lumen of the palisade cell is large at the base and tapers toward the top, being very narrow in the upper part of the cell owing to pronounced thickening of the cell walls. The radiating character of the cavity at the top of the cell can be seen

in surface view, while at the base the cell is thinner walled and the broad lumen is circular or oval in outline.

Beneath the palisade cells is a subepidermal layer of cells that are usually broad at the base with intercellular spaces at their outer limits. They are about 6μ high in most parts of the seed coat and very broad, ranging up to 30μ . These hour-glass or I-shaped cells are characteristic of many legumes and are sometimes referred to as "osteosclerids." Their basal portion is somewhat broader than the outer part, and the thick walls have deep pits and longitudinal striations so that the surface view presents a radiating pattern.

Under the subepidermal cells is a parenchymatous zone which consists of several layers of much compressed cells that are periclinally elongated and thin-walled. The outermost layers are without intercellular spaces while the inner ones are commonly spongy in their arrangement. The endosperm has a distinct outer layer of aleurone cells, and underlying it is a zone of large thin-walled parenchymatous cells which become mucilaginous following the intake of water. The epidermal cells of the cotyledon are small, and the mesophyll usually consists of three layers of palisade cells and several rows of spongy cells. The cotyledons are high in protein content, and fat and starch may also be present.

The occurrence of impermeable or "hard" seeds is not uncommon. The percentage of such seed in commercial lots may be high enough to constitute a real problem in alfalfa production, as in Colorado, where, over a period of years, it was found that approximately 22 per cent of the seed was of that type. The impermeable seeds fail to imbibe water and germinate within a reasonable length of time, and various methods have been used to overcome this condition. These include treatments with hot water, sulphuric acid, scarification, and the application of dry heat. In relating this problem to the structure of the seed coat, Lute (18) determined that it is not the cuticle which is the impermeable layer, but that this characteristic resides in some peculiarity of the outer portion of the palisade cells, although no structural or mechanical differences between permeable and impermeable seeds were discovered.

DEVELOPMENT OF THE SEEDLING. — In germination, the primary root emerges near the hilum and penetrates the soil rapidly, forming a slender unbranched tap root. The seedling is epigeal, in contrast to the hypogeal pea; and the oval cotyledons are raised above the

ground as the hypocotyl elongates and straightens. The first epicotyledonary leaf is simple and obcordate or orbicular with a very slender petiole, while the second, third, and subsequent leaves are trifoliate. (Fig. 161.)

The seedling axis is slender with a short first internode, but the second one may elongate very greatly as the plant matures. There are buds in the axils of the cotyledon as well as in the axil of each foliage leaf, and these develop coincident with the growth of the

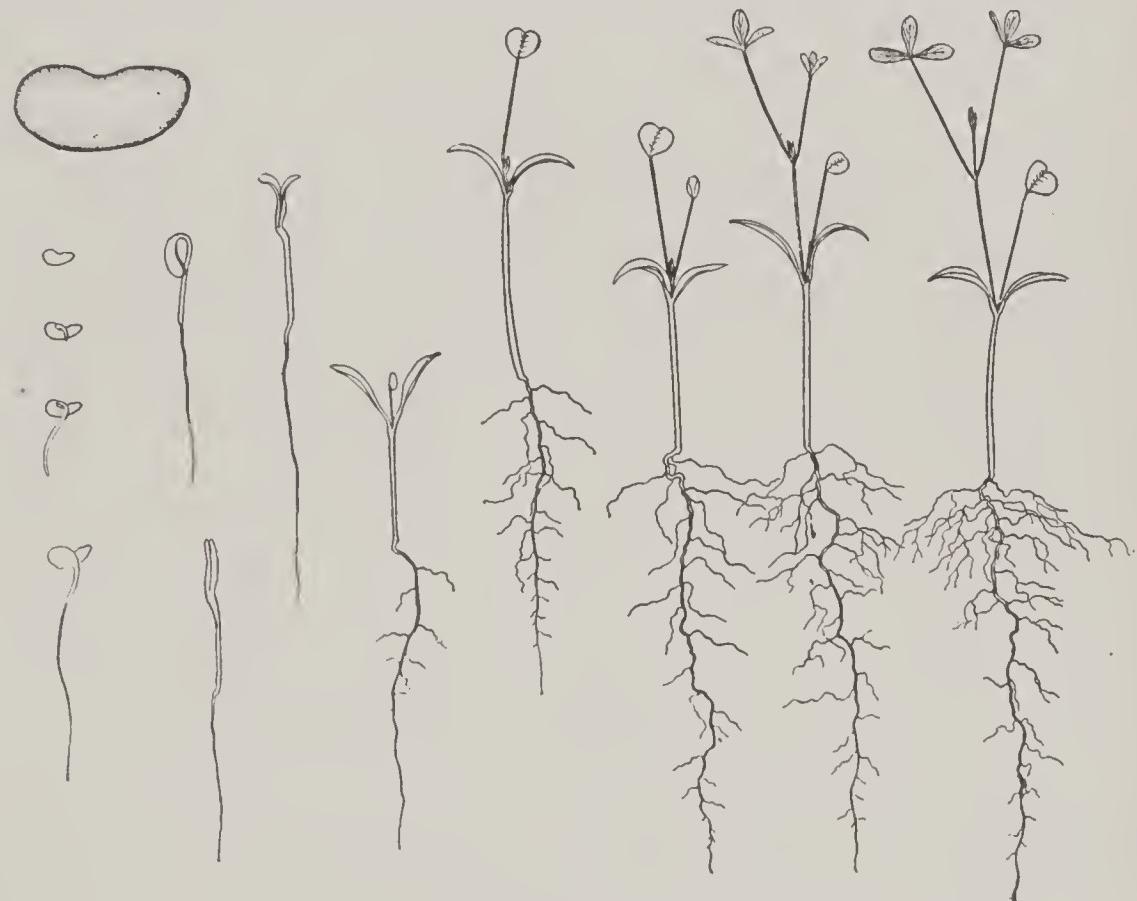


FIG. 161. Stages in development of seedling in Grimm alfalfa.

primary axis to form a "crown." This term has been used by Stewart (29) to include the perennial portions of the stems of the plant.

Very commonly, there are three or sometimes four branches, in addition to the primary axis, which form this characteristic crown. When four develop, the fourth arises from the axillary bud of the first trifoliate leaf, following the development of the other three from the cotyledonary buds and that of the unifoliate leaf. (Fig. 162, A.) In the case of vigorously growing plants, additional branches may arise from adventitious buds which occur near the bases of the axillary branches, the first one usually developing

between the branches arising from the buds in the axils of the cotyledons. Several buds may develop from any point in the circumference of the crown stem at this level, or even higher up on the axis when the plants have become embedded in the soil. (Fig. 162, B.)

In very large crowns which have many small stems, it appears that these arise in part adventitiously and in part from buds in the axils of bracts and basal leaves. Jones (15) has pointed out that the behavior of the plant in regard to the development of the crown

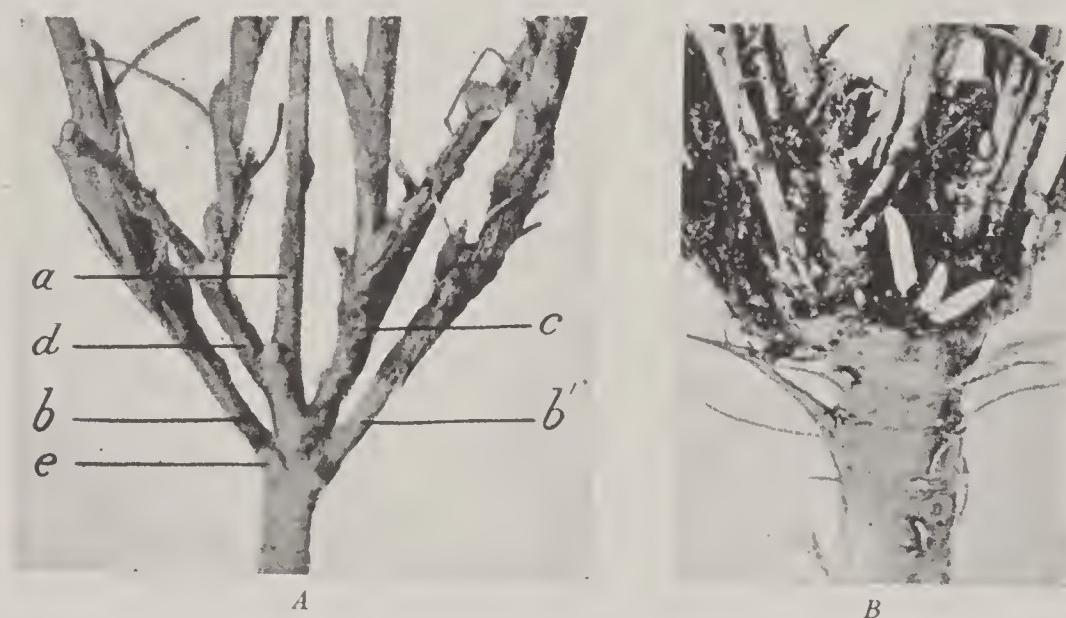


FIG. 162. A, symmetrical crown of a hardy alfalfa plant at end of its first winter: *a*, first seedling stem; *b* and *b'*, stems from axils of cotyledons; *c*, stem from axil of unifoliate leaf; *d*, stem from axil of first trifoliate leaf; *e*, first bud from base of crown, arising between stems from axils of cotyledons and opposite the stem from the lowest seedling bud: B, crown and portion of tap root of an uninjured alfalfa plant from a 4-year-old field at Madison, Wisconsin. (After Jones, *Jour. Agr. Res.*)

is variable, depending upon the variety, the vigor of the plant, and environmental conditions. Where the seedling is buried deeply, the first branches of the crown may arise from axillary buds higher up on the primary axis; and where a plant after forming a crown is buried more deeply, a new crown may form higher up. No buds arise from the root portion of the axis in cases where it may become exposed.

THE PRIMARY ROOT. — The stele of the primary root is triarch or rarely tetrarch. The protoxylem abuts the pericycle and the primary xylem is differentiated centripetally until a continuous xylem strand is formed. The number of protoxylem elements in each arm is usually limited to three or four annular and spiral

vessels; and, in most cases, there is a large, centrally located, reticulate metaxylem vessel which may or may not be in direct contact with the protoxylem at all points. Three primary phloem groups develop between the xylem arms, and the peripheral phloem cells differentiate as fibers adjacent to the pericycle. (Fig. 163.) The pericycle is uniserial at first; but early in ontogeny, there may be tangential divisions of the cells outside the protoxylem points, and later the entire pericyclic region becomes multiseriate.

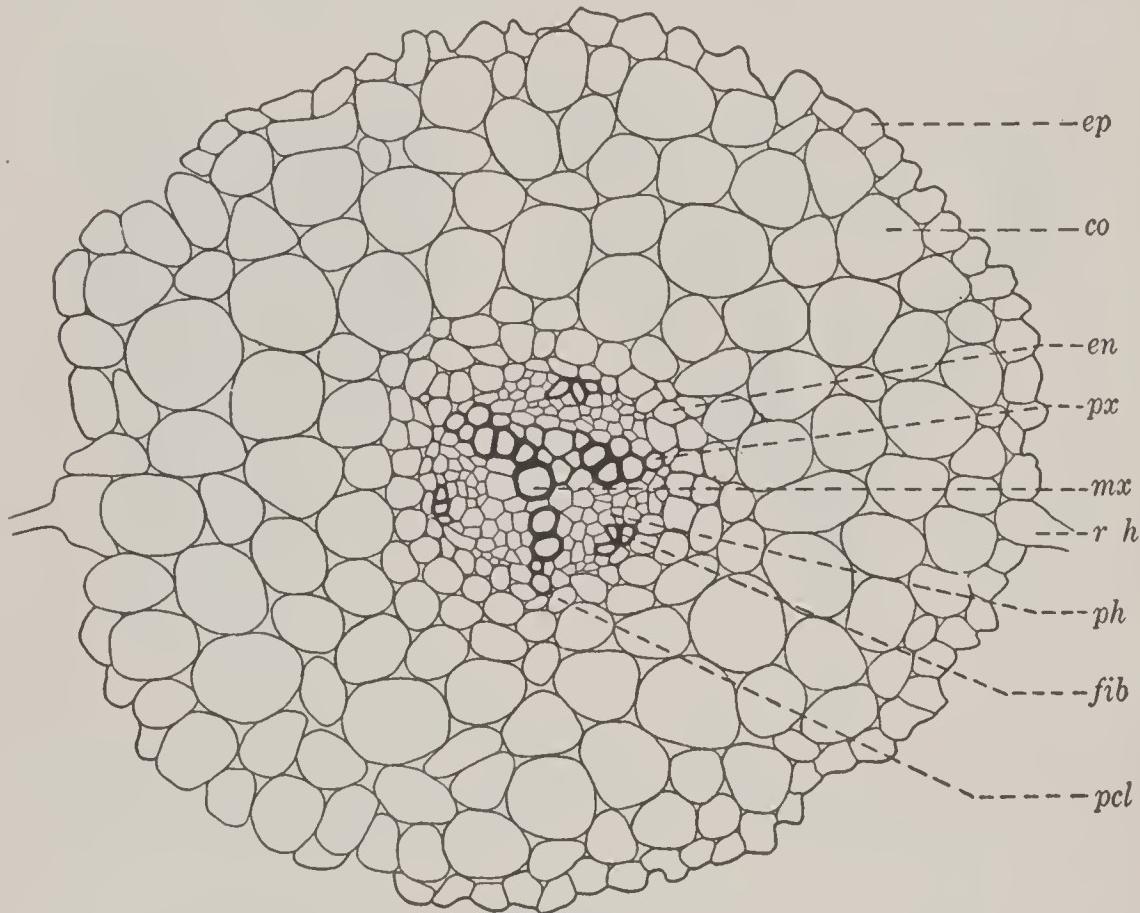


FIG. 163. Transection of young primary root showing triarch xylem: *co*, cortex; *en*, endodermis; *ep*, epidermis; *fib*, phloem fibers; *mx*, metaxylem; *pcl*, pericycle; *ph*, phloem; *px*, protoxylem; *rh*, root hair.

The cortex consists of an endodermis and four or five layers of large parenchymatous cells which are limited outwardly by the epidermis. Lateral roots originate in the pericycle on the same radii as the protoxylem points so that they are arranged in three longitudinal rows, except in cases where the root is tetrarch.

VASCULAR TRANSITION. — The vascular system of the seedling axis has been investigated by van Tieghem (32), Compton (8), Winter (36), and others. Unlike the pea, the transition is entirely hypocotyledonary, and the reorientation of the vascular tissues

from the exarch radial to the endarch collateral arrangement is completed in the veins of the cotyledons. Both van Tieghem and Gérard (13), in describing the vascular anatomy of the primary root and hypocotyl, state that two of the xylem groups of the triarch root are continuous with the cotyledonary bundles, while the third strand passes through the cotyledonary plate and continues as a trace to the first epicotyledonary leaf. On the other hand, Compton and Winter find no direct continuity between the primary vascular tissues of the root and hypocotyl and those of the epicotyledonary system. They ascribe van Tieghem's interpretation to a study of older seedlings in which the differentiation of the vascular tissue is advanced to a point where the downwardly diverging foliar traces are anastomosed with the hypocotyledonary portions of the cotyledonary traces.

The lower portion of the primary root is commonly triarch, but a tetrarch arrangement is evident beginning approximately at the region of the collar. (Fig. 164, A, B.) At about this point, one of the three xylem arms appears somewhat smaller than the other two and the angular divergence of the latter pair increases until it approximates 180° . These two rays, which can be designated as the polar xylem, lie in the cotyledonary plane. The third ray occupies a position at right angles to the cotyledonary plane, and a fourth protoxylem group is differentiated which lies in the intercotyledonary plane opposite the third ray. Thus, at the base of the hypocotyl, the stele is commonly tetrarch with two large xylem points in the cotyledonary plane and two smaller ones occupying the intercotyledonary one. (Fig. 164, C, D.) During this development, a fourth phloem group is differentiated, and the four primary phloem strands occupy positions alternate with the xylem.

At higher levels in the hypocotyl, the four phloem groups are divided into eight groups, and these are oriented in a more nearly collateral position with respect to the xylem. (Fig. 164, E, F.) A few millimeters below the cotyledonary plate, the polar metaxylem elements are reoriented to form two V-shaped groups which, with the polar protoxylem, constitute the triad structure of each cotyledonary bundle. (Fig. 164, G, H.) Coincident with the reorientation of the pattern of the vascular tissues in the upper hypocotyl, a central pith is differentiated; and cell enlargement and division result in an increase in the diameter of the hypocotyledonary axis. It has been suggested by Jones (15) and Rim-

bach (28) that this radial enlargement may result in a marked shortening of the hypocotyl.

According to Winter (36), the polar protoxylem elements,

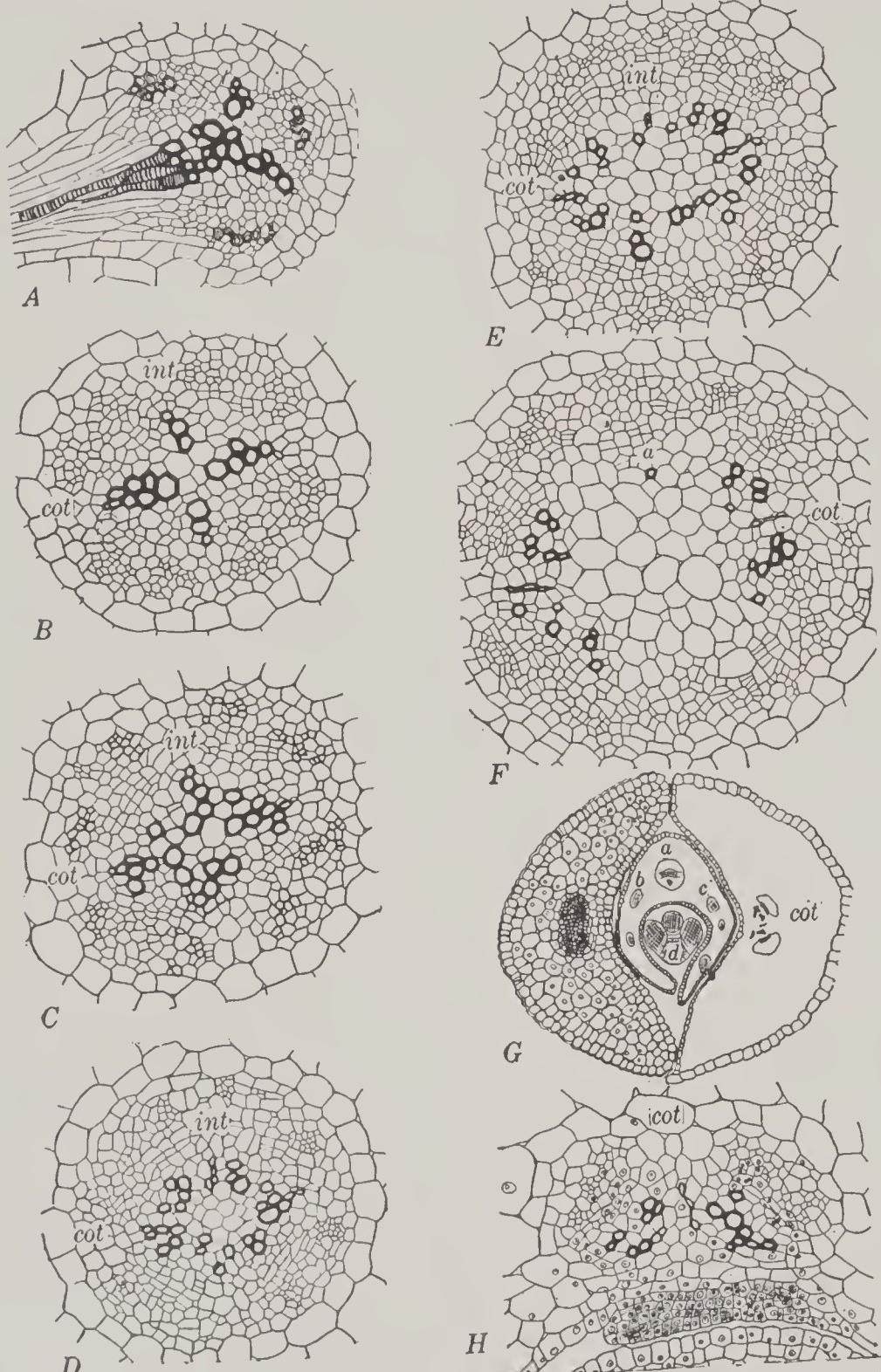


FIG. 164. *A*, triarch root of alfalfa showing lateral root formation; *B*, tetrarch stage; *C*, *D*, *E*, bifurcation of metaxylem and formation of pith; *F*, cotyledonary node below point of divergence of cotyledons; *G*, transection of cotyledons and epicotyl; *H*, triad bundle of cotyledon; *cot*, cotyledonary plane; *int*, intercotyledonary plane; *a*, *b*, *c*, bundles of first foliage leaf; *d*, median bundle of second foliage leaf. (After Winter.)

although much stretched by the rapid elongation of the hypocotyl, retain their identity and position in the cotyledonary plane, while those in the intercotyledonary plane eventually become disorganized and disappear. With the exception of the intercotyledonary protoxylem, all the primary xylem of the root forms a continuous system with that of the cotyledonary traces. The situation is somewhat complex because of an early initiation of cambial activity in the hypocotyl with the consequent formation of secondary xylem elements. In older seedlings, there is a further complication owing to the downward differentiation of the foliar traces of the epicotyledonary leaves which anastomose with the primary and secondary vascular tissues of the hypocotyl.

THE DEVELOPMENT OF THE EPICOTYL. — The growth of the epicotyl is usually retarded, so that the vascular system of the cotyledons and hypocotyl is well developed and secondary thickening is in progress by the time the primary vascular strands of the first foliage leaves have differentiated downward to the level of the cotyledonary node. The median bundle of the three which supply the first leaf is located in the intercotyledonary plane and consists of collaterally oriented phloem and xylem, the latter continuing as the primary xylem of the fourth ray of the hypocotyledonary axis. The two lateral bundles are located on either side of the stele, and anastomose with the secondary tissues of the hypocotyl. Branches of the lateral traces supply the stipules, and the main laterals continue up the petiole, anastomosing with the median bundle above the point where the stipules are diverged from the petiole. Nearer the lamina, the bundles separate again and continue in the petiole as three parallel and distinct veins.

In the first, unifoliate leaf, the three bundles anastomose and enter the blade as a single bundle. In the second, trifoliate leaf, and in subsequent leaves, the terminal leaflet is supplied by the median bundle and the lateral bundles enter the lateral leaflets. There are cross-branches between the median and lateral bundles, each of the latter receiving a branch from the median bundle, and giving off a strand which joins the median bundle, after penetrating for a distance into the terminal leaflet. (Fig. 170, A.) The median bundle of the second leaf lies opposite that of the first leaf; and, like the latter, anastomoses with the vascular system of the hypocotyl at or slightly below the cotyledonary node.

SECONDARY THICKENING OF THE Root. — Secondary thickening follows maturation of the primary tissues; and, in the main roots which may become several years old, a massive woody axis is formed. Cambial activity results in the formation of three, or four, wedge-shaped sectors of secondary xylem which are separated by broad parenchymatous rays that extend radially from each protoxylem point toward the periphery. These main primary rays are pericyclic in origin, but there are also broad secondary xylem rays in each of the major sectors. (Fig. 165.)

Jones (15) has described the annual rings formed in the development of the tap root in connection with studies of winter injury, and points out that they may be distinguished readily in most instances. Exceptions occur in plants grown under dry farming conditions, such as those of western Kansas, where the annual increments of secondary growth are small and of uniform character; and, also, in regions like southern California, where the plants do not become dormant in the winter. The demarcation of the rings is evident because the late summer and autumn growth of xylem is characterized by vessels of small diameter and small uniform parenchymatous cells with relatively few or no interspersed fibers, while the spring wood has larger vessels, less parenchyma, and numerous fibers. The fibers are arranged in groups separated by zones of vessels and tangential bands of parenchyma, so that these layers may sometimes be mistaken for annual rings. (Fig. 165.) In old roots, the enlargement and division of the parenchymatous cells located near the center of the axis result in the separation of the primary xylem elements from the adjacent secondary xylem and from each other.

The annual increments of secondary phloem are not as large as those of xylem, but they are well defined. This is because the first elements to be differentiated each growing season are phloem fibers, while, later in the summer, fiber formation is followed by the development of sieve tubes and parenchyma. With the production of each succeeding group of phloem fibers, there is a tendency for the sieve tubes and parenchyma of the preceding year to be crushed; and although each annual increment of phloem consists of a group of fibers, sieve tubes, and parenchyma, the last two may be somewhat obliterated. Jones (15) has noted that the secondary xylem of the first year has fewer fibers than occur in succeeding years, and this is true also of the secondary phloem of

the first year which consists of a few scattered strands produced early in the year and a larger group of fibers formed later in the same season.

The cortical and epidermal tissues do not persist for any great length of time, since the cells of these zones are ruptured and disintegrated by secondary activity. For this reason, the outermost portion of the mature root consists of a pericyclic region

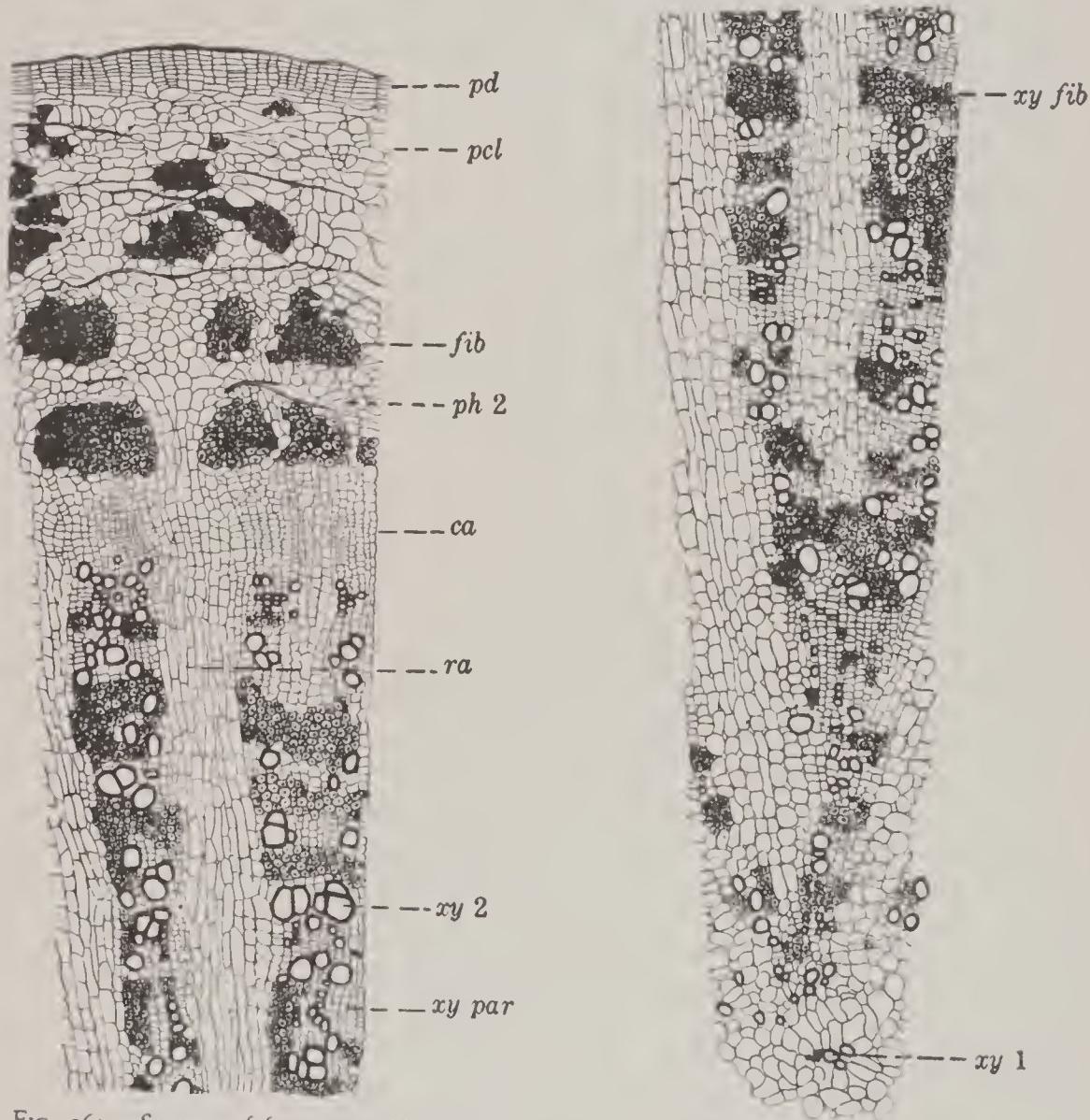


FIG. 165. Sectors of four-year-old tap root: at left, showing the outer portion; and at right, the inner portion of root. Each annual addition in growth may be distinguished in both xylem and phloem. In xylem, the spring wood has relatively large vessels and abundant fibers. The late autumn wood has few or no fibers and small vessels surrounded by xylem parenchyma. The end of each annual cycle is marked by an abrupt transition from small to large vessels. In phloem, a bundle of fibers is laid down in spring, when the xylem is also producing fibers. Sieve tubes and parenchyma are produced in late summer and fall, only to be crushed as soon as the next fibers are produced in spring: *ca*, cambium; *fib*, phloem fibers; *xy 2*, secondary xylem; *xy fib*, xylem fibers; *xy par*, xylem parenchyma. (After Jones, *Jour. Agr. Res.*)

in which the cells are much elongated tangentially, and the external layers of the pericycle function as an active phellogen producing a well-defined periderm of regularly arranged and flattened cells. Scattered lenticels may occur over the surface of the root.

In connection with a study of the plugging of alfalfa roots caused by wilt or root rot, LeClerg and Durrell (17) have described the tissues of the root. In the secondary xylem, the vessel segments are very short and the walls are densely beset with bordered pits. These are transversely elongated, in some instances to such an extent that the wall appears to have scalariform or reticulate thickenings while in others the pits are more nearly circular in outline. The end walls of adjacent vessel segments are perforated with many minute pores. The walls of mature fibers are so thick that the lumen of the cell is nearly occluded.

Graber and his coworkers (14) have pointed out that, "The alfalfa plant has a high metabolic activity, with great ability for regeneration; and its reserves are rapidly reduced by frequent cuttings." There is a marked difference in alfalfa roots grown under environmental conditions and cultural practices which produce high reserves as compared with those which result in low reserves. In general, roots of high reserve plants have a greater proportion of parenchyma in relation to the fibrous tissue; and the parenchymatous cells are packed with reserve foods, principally starch.

Root NODULES. — The general considerations regarding the root nodules of the Leguminosae, including method of infection, the penetration of the bacteria into the tissues, and the growth of the nodule, are discussed in the succeeding chapter on *Pisum*, but certain points specifically dealing with the nodules in *Medicago* deserve mention.

Thornton (30) has investigated the early development of the nodule in alfalfa and on the basis of Milovidov's (21) classification of types of infection, places *Medicago* in type I in which "most, if not all the cells of the infected region receive their bacteria by separate intrusions of the infection thread." The infecting organism in this case is *Rhizobium meliloti* which, according to Fred, Baldwin and McCoy (10), is apparently specific for the alfalfa group, including six species of *Medicago*, three of *Melilotus*, and one of *Trigonella*. The bacteria usually enter

the root hair at its distal extremity, although occasionally penetration may be effected through other epidermal cells. Within the root hair, they form infection threads and these penetrate to the inner layers of the cortex, but Thornton states that they do not enter the endodermis.

As a result of bacterial invasion, the cells become more densely protoplasmic, their nuclei enlarge, and cell division ensues. The actively dividing area involves two or three layers of cells on either side of the infected cells, and this suggests that division is induced by some substance diffused from the infection thread. Cell divisions occur not only in the cortex but to some degree in the endodermis and pericycle. The infection thread continues to grow and penetrates the newly formed cells or it may form zoogloal masses from which the infection thread continues to grow. There is a rapid multiplication of the bacteria in the bacteroidal tissue and certain form changes occur in them so that they increase in size and become banded. It is thought that the banded rods represent a stage which is significant in nitrogen fixation.

When the infected cells cease to divide, they enlarge to approximately twice their original size, become vacuolated, and ultimately form a large central vacuole. While cell enlargement is being initiated in the central and basal regions of the nodule, a meristem persists at its distal end which causes it to increase in length and to assume a cylindrical form. Thornton (31) has measured nodules at various ages and finds that those two weeks old average 1 mm. in diameter with a length of 1.3 mm. Increase in diameter is rapid for the first two days, and the nodule reaches a relatively constant diameter at the end of the first week, when its length begins to exceed the breadth. The development of vascular strands in the nodule is similar to that described by Brenchley and Thornton (3) for *Vicia Faba*. (See *Pisum*, Chapter XII.)

Fred, Baldwin, and McCoy (10) have pointed out that the nodule is

"distinctly not a modified lateral root, for it has no central cylinder, root cap, nor epidermis. Furthermore it does not digest its way out from the cortex of the main root but remains covered with a considerable layer of cortical parenchyma. Anatomically then, it differs from non-leguminous nodules, many of which are clearly modified roots."

Probably the correct interpretation of the nodule is to consider it as a parenchymatous outgrowth of the root that is connected with it by a system of vascular bundles which provide for the translocation of material. Its development results from a meristematic activity of the cells which is induced by and is a response to the stimulation of the invading bacteria.

THE YOUNG STEM. — The young stem is approximately square in transection with a pith consisting of large, compactly arranged, parenchymatous cells that are continuous with those of the cortex through the medullary rays. The major bundles are located at

the angles of the axis with the smaller ones occupying the intervals between. All of the bundles are collateral, the phloem being limited outwardly by strands of elongated, thick-walled pericyclic fibers which, with the lignified xylem elements and the collenchyma, constitute the mechanical system of the stem. The pericyclic fibers do not form a continuous zone around the stele, but constitute a series of strands or tangentially extended sectors abutting the endodermis. The sieve tubes are long and narrow with simple sieve plates in their end walls; and with them are companion cells and

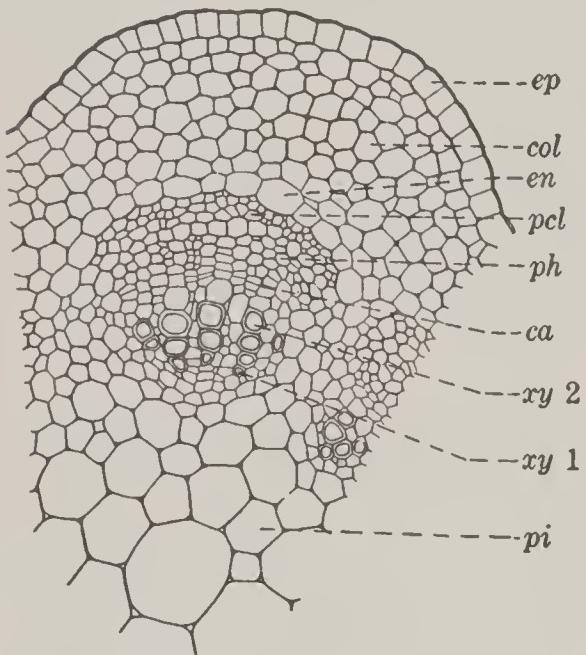


FIG. 166. Transection of sector of young stem showing vascular bundle: *ca*, cambium; *col*, collenchyma; *en*, endodermis; *ep*, epidermis; *pcl*, pericycle; *ph*, phloem; *pi*, pith; *xy 1*, primary xylem; *xy 2*, secondary xylem.

parenchyma. The primary xylem elements have spiral thickenings, the secondary xylem consists of radial rows of vessels with oval bordered pits, and between the rows are fibers and wood parenchyma. (Fig. 166.)

The cortex is limited centripetally by endodermal cells that usually lack Casparyan thickenings. They can be recognized by their size and starch content, as well as by the occurrence of crystals of calcium oxalate which frequently form late in ontogeny. In transection, they appear as a continuous row of rectangular or oval, non-chlorophyllose cells that are conspicuously larger than the pericyclic cells centrad to them. Outside the endodermis

is a zone of chlorenchyma; and this is limited peripherally by collenchyma which is one layer in width, except at the angles of the stem. A strand of collenchyma reinforces the stem at these points, and may project to form a more or less pronounced longitudinal ridge. In some instances, it extends from the epidermis to the endodermis so that the continuity of the chlorenchyma is interrupted. The collenchymatous cells are thickened at their angles and about as long as the epidermal cells.

The epidermal cells are elongated in the axial direction and are somewhat irregular in shape. There are numerous stomata, Wilson (35) reporting approximately 300 to the square millimeter. Two types of epidermal hairs may develop, one being glandular and two or more celled, while the other is an elongated, slender, unicellular trichome similar to that found on the leaves. The glandular hairs, which are not commonly found among other genera of this tribe, occur in a frequency of approximately 24 per square millimeter, and the unicellular ones are somewhat more numerous.

THE MATURE STEM. — As secondary thickening proceeds, an interfascicular cambium develops, and a cambial cylinder is formed which produces a continuous zone of lignified xylem. The connective tissue cut off by the interfascicular cambium consists chiefly of wood parenchyma, while the fascicular cambium continues to produce vessels, fibers, and xylem parenchyma. (Fig. 167.) As maturation continues, some of the smaller parenchymatous cells on the inner face of the bundles may become lignified, forming an uninterrupted zone of mechanical tissue in conjunction with the connective tissue produced by the interfascicular cambium. This band of lignified parenchyma frequently encloses a zone of thin-walled parenchyma which surrounds the protoxylem elements of each bundle. The parenchymatous cells of the pith may disintegrate or become ruptured so that the mature stem becomes hollow. The inner tangential, radial, and end walls of the endodermis may become lignified, forming an almost continuous sclerenchymatous sheath. In the aerial portion of the stem, the amount of secondary thickening is not usually sufficient to cause any splitting of the epidermis and cortex; but, when this does occur, a cortical phellogen develops.

THE UNDERGROUND STEM OR RHIZOME. — The extent to which the underground portion of the crown stem may develop is vari-

able, depending upon the variety of alfalfa and, to some degree, upon cultural practices and climatic conditions. Garver (12) has

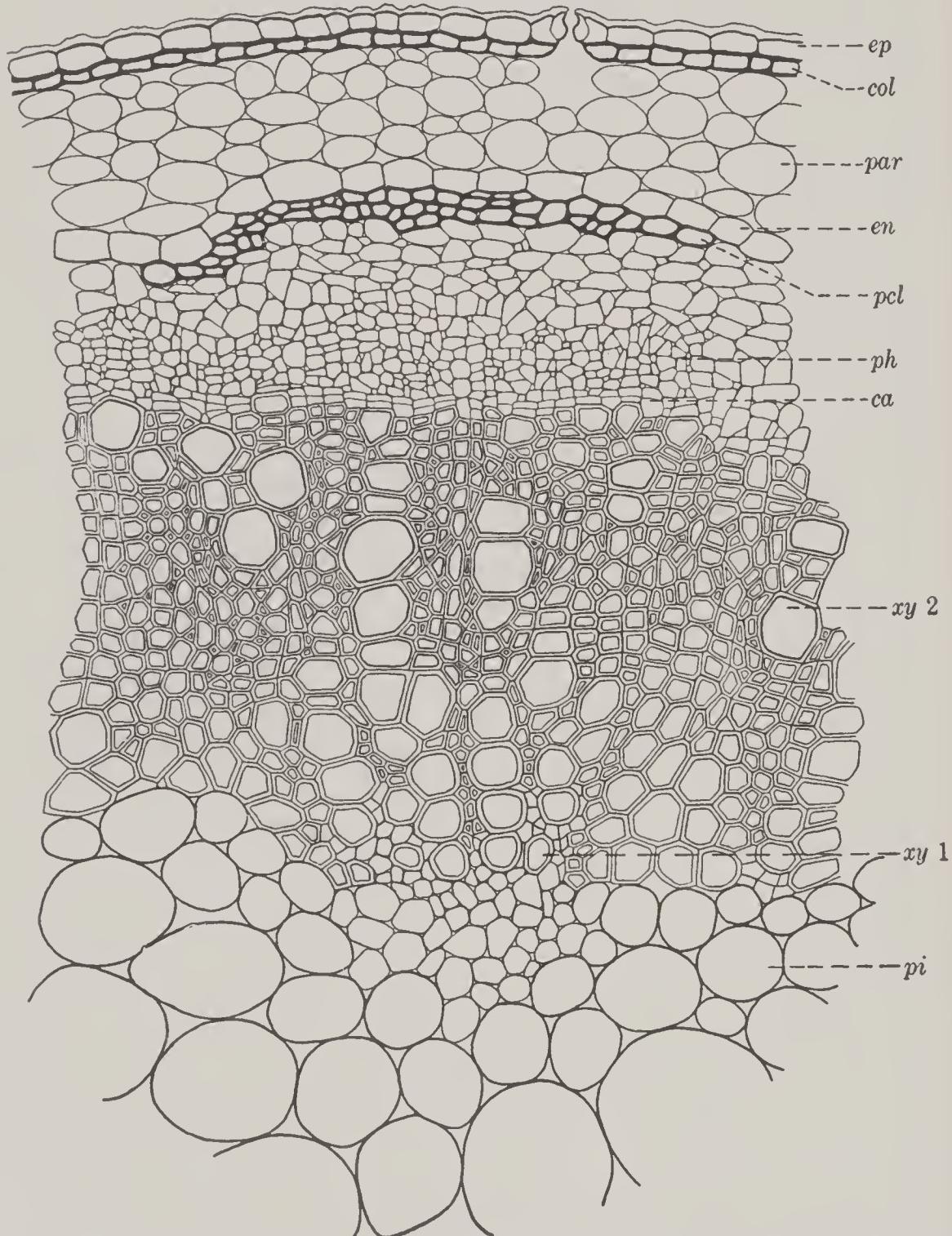


FIG. 167. Transection of sector of old stem: *ca*, cambium; *col*, collenchyma; *en*, endodermis; *ep*, epidermis; *par*, cortical parenchyma; *pcl*, pericycle; *ph*, phloem; *pi*, pith; *xy 1*, primary xylem; *xy 2*, secondary xylem.

pointed out that most of the southern-grown forms have relatively few rooting rhizomes; while in the northern-grown, variegated alfalfas, especially Grimm, the rhizomes are often well devel-

oped, although not as much so as in the yellow-flowered, *M. falcata*.

The structure of the rhizome resembles that of the aerial portions in the general arrangement of the tissues, but there are certain definite specializations which may be related to the soil environment, and to the greater age that the underground portions usually attain. One important difference lies in the formation of well-defined Casparyan thickenings in the endodermal layer of the rhizome, followed later by a pronounced lignification of the radial and inner tangential walls.

Another development that does not commonly occur in the aerial stem takes place in the pericyclic zone, where several layers of parenchymatous cells develop between the endodermis and the sectors of pericyclic fibers. As the rhizome increases in diameter, the cells in this zone adjacent to the endodermis function as a phellogen, producing a periderm which serves as the protective layer when the epidermis and cortex are destroyed. (Fig. 168.) Jones (15) has noted this development in the endodermis of the perennial portion of the stem, and attributes the origin of the phellogen to this layer rather than to the pericyclic cells centrad to it. He states that

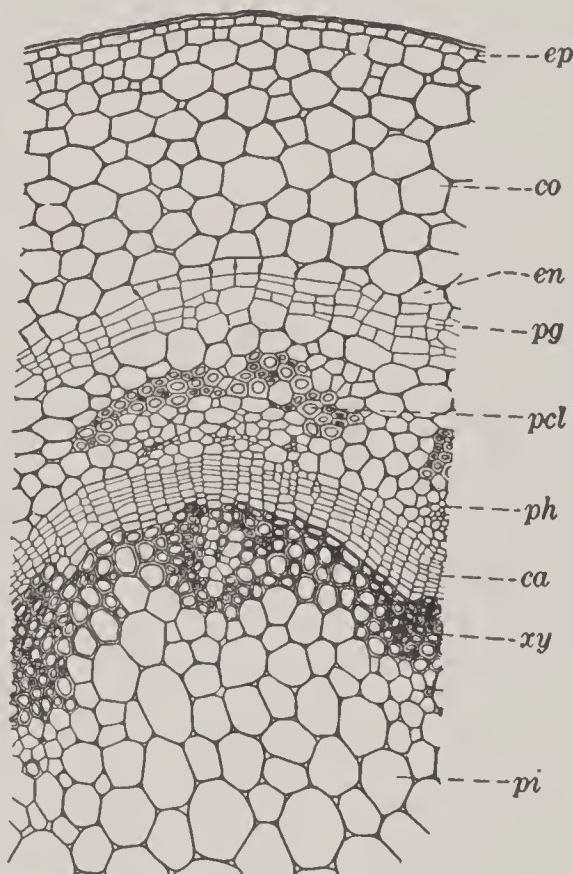


FIG. 168. Sector of rhizome showing detail of vascular ring: *ca*, cambium; *co*, cortex; *en*, endodermis; *ep*, epidermis; *pcl*, pericyclic fibers; *pg*, phellogen; *ph*, phloem; *pi*, pith; *xy*, xylem.

"When the cambium begins to produce secondary growth the endodermis becomes a phellogen. The portions of the endodermal cell walls inside the thickenings, if any have been laid down, expand conspicuously, and almost simultaneously two or three cross walls are laid down interior to these thickenings. Hereupon the epidermis dies, separates from the cortex, and forms the brown membranous covering often seen on young stem bases early in spring. The phellem

originating from the endodermis becomes the effective outer covering, both in the large crown branches from axillary buds and in the small stems."

THE VASCULAR ANATOMY OF THE STEM. — Nägeli (23) has classified the genus *Medicago*, on the basis of its phyllotaxy and vascular anatomy, in the type in which the leaves alternate in two rows and the leaf trace consists of three bundles which pectinate with the traces of both rows. The median bundle divides at the base of the leaf into three branches of which the smallest central branch enters the petiole, while the lateral ones anastomose with the two lateral bundles of the trace forming the bundles which supply the stipules.

Upon entering the stem, the median bundle extends down through two internodes without branching. It then curves slightly to one side from its original position in an angle of the stem; and, just below this point of curvature, forks into two branches. These anastomose with the lateral bundles of the next lower leaf trace. The two lateral bundles of each leaf trace extend downward in the corners through their own internode; and, at the next node, enter the vascular ring alternating with the lateral bundles of the next lower trace. Each of them then unites with a branch of the median bundle of the next higher trace, and extends with it through two internodes. In the third internode, this bundle finally anastomoses with a lateral bundle of the second lower trace. Where there is an axillary bud, it is supplied by two bundles which extend separately through one internode, and anastomose at the next node with the lateral bundles supplying the next higher leaf. (Fig. 169.)

THE LEAF. — The general structure of the stipulate, pinnately compound leaf, and the course of its vascular bundles have been described. Above the stipules, the three petiolar bundles extend to the point of divergence of the short petiolules of the leaflets where the terminal leaflet receives the median bundle, and the lateral bundles become the midveins of the lateral leaflets. There are branch veins between the three major bundles at this point so that the three major veins of the leaflets are cross-connected. (Fig. 170, A.) In each elliptical or oval leaflet, the midvein extends throughout its entire length, and the lateral branches are pinnately arranged. These rebranch to form a net-veined system in which the ultimate veinlets end in the mesophyll, but

some of the major lateral veins extend directly to the margin of the leaflet, terminating in the prominent teeth which occur at its

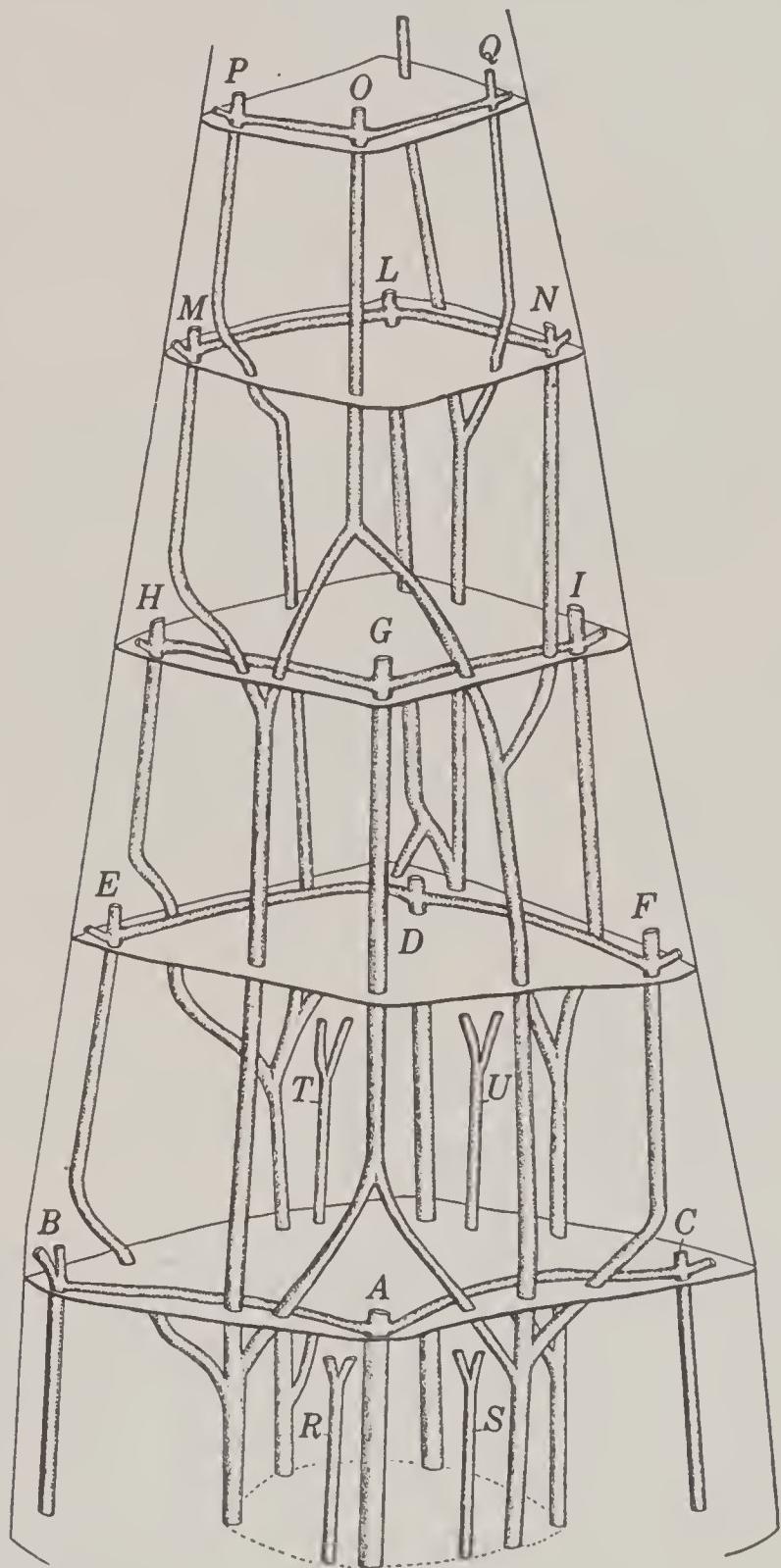


FIG. 169. Schematic representation of bundles near apex of stem showing vascular anatomy of five nodes and internodes in *Medicago-Lathyrus* type. Each leaf is supplied by a median bundle and two laterals, and the alternate phyllotaxy of leaves is indicated by departure of traces ABC, DEF, GHI, LMN, OPQ. The bundles R, S, T, U supply axillary buds. (Diagram based on Nägeli.)

tip. Wilson (35) observed beads of water accumulating on the teeth under some conditions, and has suggested that these terminations might be hydathodes serving as drip tips.

The midvein of the leaflet forms a prominent ridge on its abaxial surface. The branches from it lie much closer to the lower epidermis than the upper, and, in some instances, the mechanical tissue surrounding the secondary veins is in contact with the lower epidermis. The midvein is almost completely surrounded by a bundle sheath of thick-walled mechanical cells which become

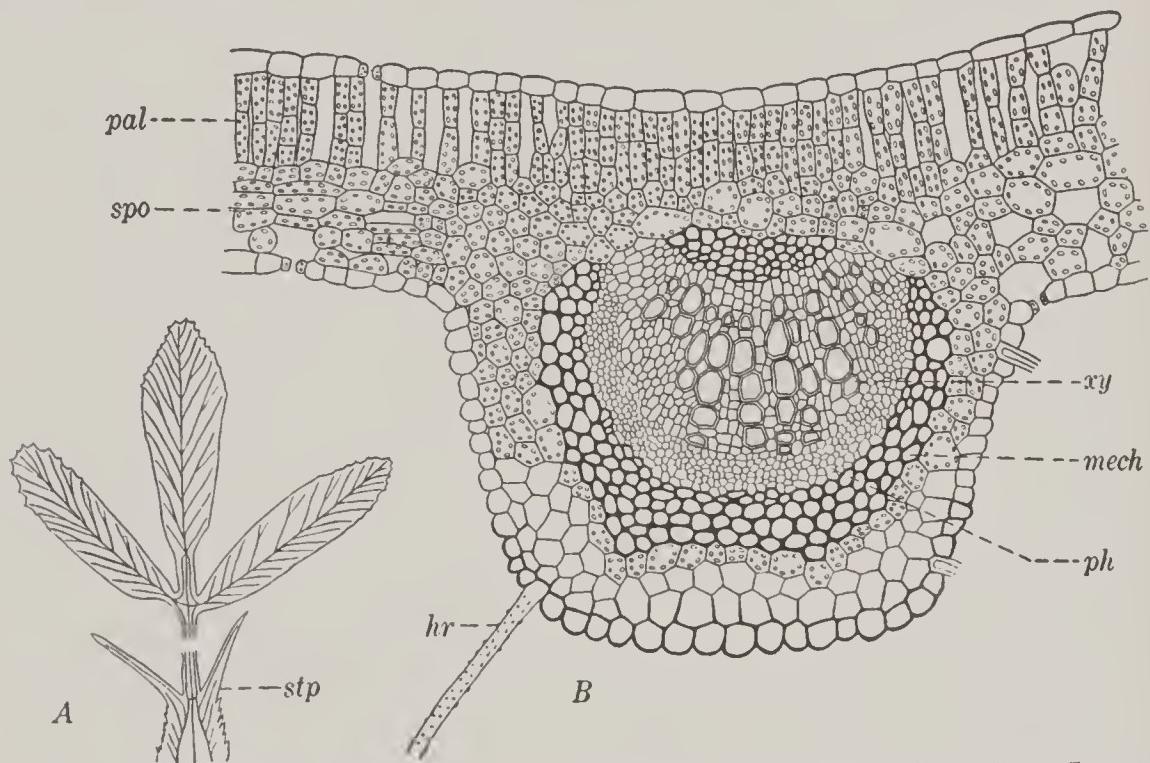


FIG. 170. A, habit of foliage leaf showing stipules and character of venation; B, transverse section of portion of leaflet cut through midvein showing distribution of chloroplasts and intercellular spaces: *hr*, hair; *mech*, mechanical tissue; *pal*, palisade region; *ph*, phloem; *spo*, spongy tissue; *stp*, stipule; *xy*, xylem.

sclerotic in the abaxial sector, and crystals of calcium oxalate are numerous in the cells of this region. (Fig. 170, B.) Toward the distal portion of the midvein and in the lateral veins, the degree of lignification of the bundle sheaths is less pronounced, and the smaller veins are surrounded by parenchymatous cells. The vascular tissues of the midvein are similar to those of the stem, and some secondary thickening occurs in the larger veins.

The mesophyll usually consists of a palisade zone of two rows of cells approximately twice as high as broad which together constitute about half of the thickness of the leaf. The spongy parenchyma is loosely arranged and air spaces communicate freely

with stomata on both surfaces. The cells of the upper epidermis are somewhat papillate with sinuous radial walls. Stomata are numerous in the lower epidermis. Westgate (34) has reported an average of 292 per sq. mm. for ordinary alfalfa, 185 for *M. falcata*, and 211 for variegated alfalfa; while Wilson (35) found considerably over twice that number, reporting up to 700 per sq. mm. The lower epidermis is similar to the upper except that there are greater numbers of hairs produced, especially along the veins. These are of two kinds, the more numerous type being a long (0.7 to 1.5 mm.) unicellular hair which is somewhat curved and arises from a small thick-walled, basal cell around which the epidermal cells form a rosette pattern. The capitate hairs are scattered and much less abundant, consisting of a stalk of two or three cells and a terminal multicellular head.

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CHAPTER XII

LEGUMINOSAE — *Continued*

PISUM SATIVUM

GENERAL MORPHOLOGY

THE pea is an herbaceous annual with a trailing, climbing, or bushy habit; and the mature stem is dwarf or tall depending upon the variety. The pinnately compound leaves are alternately arranged, and the glaucous, oval to ovate leaflets are in one to three pairs with the terminal leaflet, and occasionally the upper lateral ones, differentiated as prehensile tendrils which serve to support the plant. (Fig. 171.) At the base of the petiole are two stipules which frequently equal the leaflets in size. The leaves at the first and second nodes above the cotyledonary node develop as small trifid bracts. (Fig. 172.)

The root system consists of a main tap root with numerous laterals which may penetrate to a depth of 4 or more feet depending upon the character of the



FIG. 171. Habit of plant showing leaf characteristics. (Courtesy of the Ferry-Morse Seed Co.)

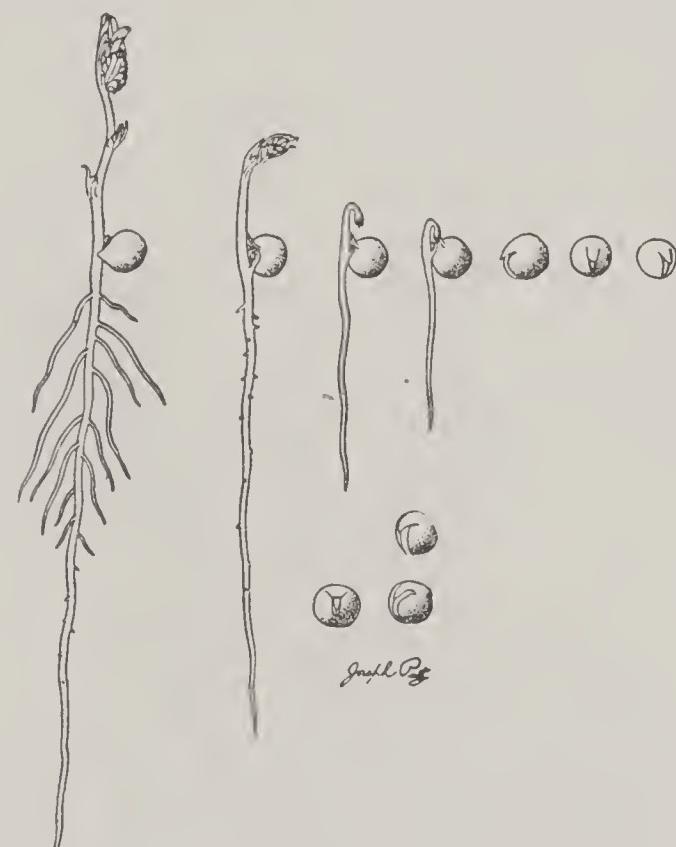
soil. Root tubercles induced by the invasion of a soil organism, *Rhizobium leguminosarum*, are often present on the root.

The inflorescence is a few-flowered axillary raceme with an elongated peduncle. In most garden peas, the flowers are white, while in field types, they are purplish, light lilac, or dull white with purple wings and a greenish keel. The calyx tube is oblique, consisting of five sepals which are undiverged at their bases, with four to five somewhat unequal marginal lobes. (Fig. 173.) The papilionaceous corolla is made up of five petals: a large broad

upper one (the standard) which encloses the others in the bud; two lateral ones (wings) which extend outward obliquely; and two lower petals (the keel) which are more or less united along their ventral edges and surround the stamens and pistil. The diadelphous stamens are ten in number, the undiverged filaments of nine of them forming an open tube which is cleft on the upper side, while the tenth, uppermost stamen is separate. (Fig. 173, E.)

The pistil consists of a single carpel, and the one-

FIG. 172. Stages in development of pea seedling.



celled; superior ovary contains two rows of ovules that arise on adjacent parallel parietal placentae so that they may appear to be in a single row. The slender style is oriented at an approximate right angle with the ovary, and the stigma is bearded on its inner or lower surface. (Fig. 173, G.) The plant is entirely self-fertile, and in nature there are probably very few instances of natural cross-pollination. Wellensiek (29) found but one case of spontaneous crossing in a period of five years, and states that "it appears that the pea is preeminently a self-fecundating plant, which is to be ascribed partly to its being scarcely visited by insects, partly to the early opening of the anthers followed by

self-fecundation, even before the flower-bud opens." In the process of early self-pollination, the anthers dehisce prior to the opening of the flower bud, and the conical point of the keel is filled with pollen as the anthers are withdrawn into its base, so that prior to anthesis the stigma is already covered with pollen.

The fruit is a legume or pod which opens along both abaxial and adaxial sutures, and the pericarp differs in the several varieties,

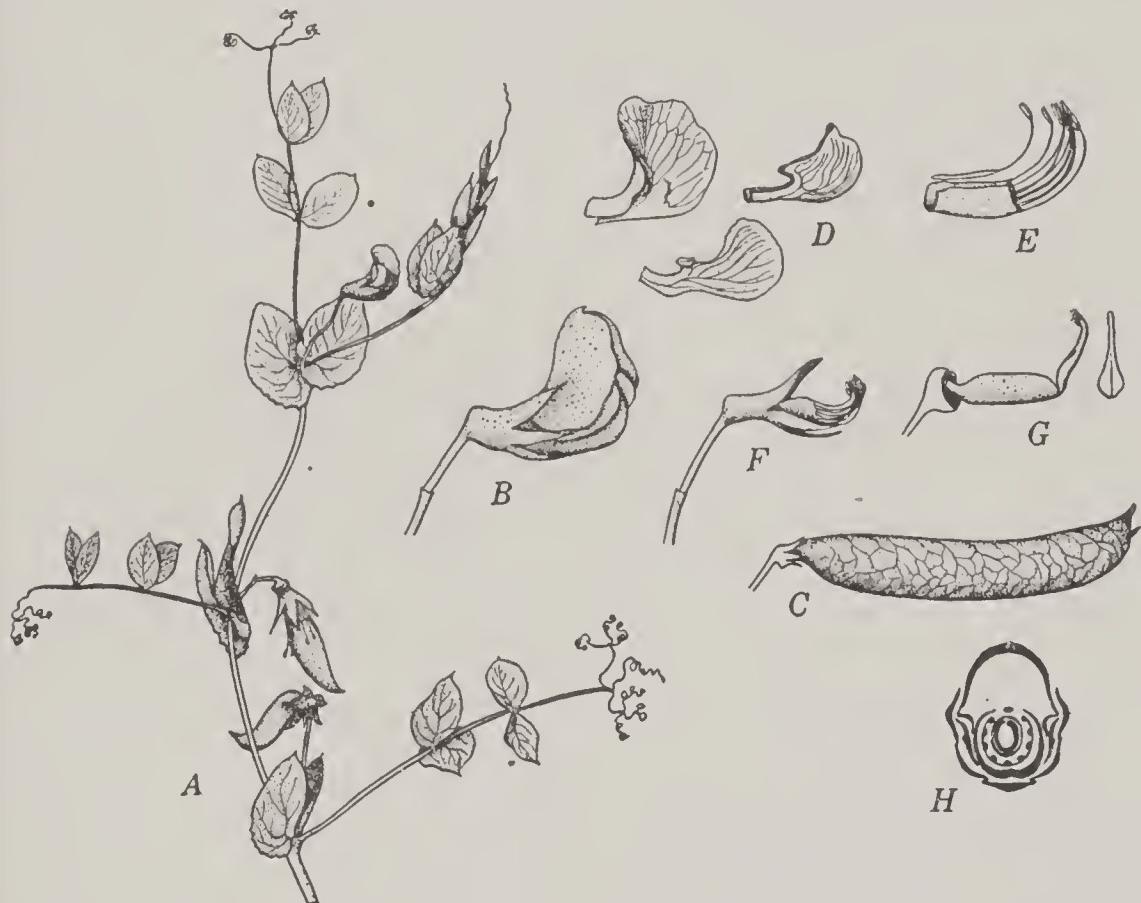


FIG. 173. *A*, habit of leaves and inflorescence; *B*, single flower; *C*, mature fruit; *D*, parts of corolla showing standard, keel, and wing; *E*, stamens, showing position of free stamen; *F*, flower with corolla removed; *G*, young carpel; *H*, floral diagram.

especially with respect to the character of the endocarp or inner surface of the ovary wall. In the edible-podded or sugar pea, the endocarp remains soft and succulent, and the ripe pods do not dehisce, while in the shelling peas, it becomes hard and dry and the pod splits open at maturity. Other differences with respect to the fruit are variations in the thickness of the ovary wall and in the shape and size of the pod, which may be curved or straight with a blunt or acute apex. The pods of some of the larger varieties attain a length of 18 cm. and a width of 2.5 cm.

ANATOMY

THE SEED. — The mature seeds are large and globular with a thin seed coat which encloses an embryo consisting of two fleshy, hemispherical cotyledons, a well-developed hypocotyl, and an epicotyl with the first foliage leaves, or trifid bracts, already differentiated. The seeds vary greatly with respect to color, degree of smoothness, and the character of the reserve foods contained in the cotyledons.

The structural details have been described by Pammel (22), Winton (34), Tschirch and Oesterle (28); and other investigators

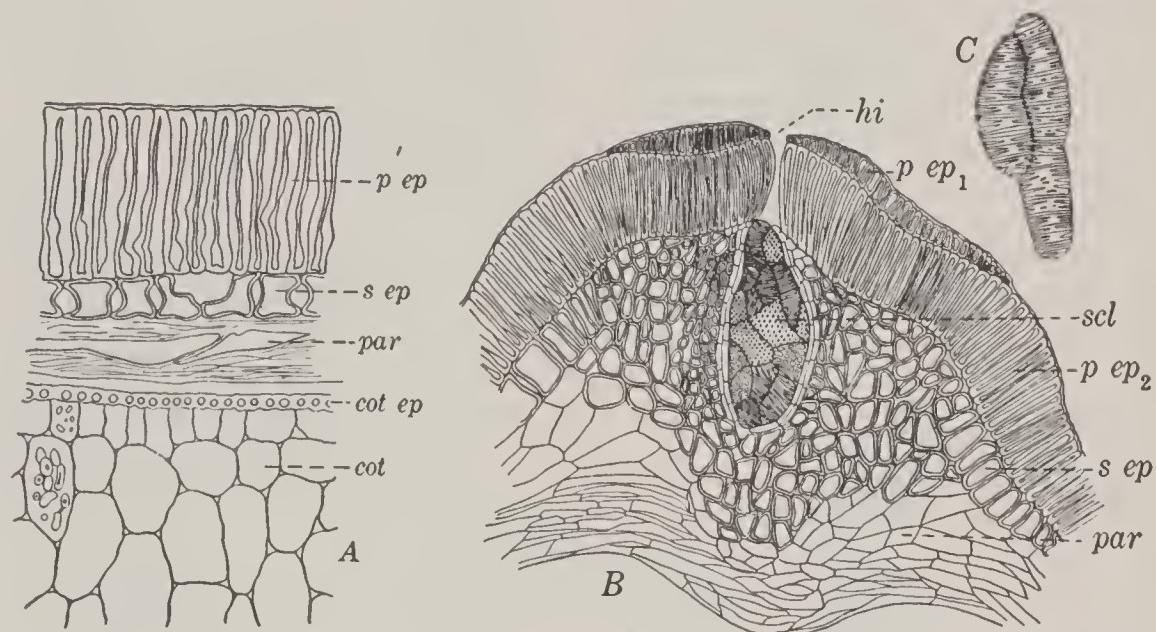


FIG. 174. *A*, section through seed coat and portion of cotyledon; *B*, section through seed coat in region of hilum; *C*, enlarged detail of porous sclerenchyma beneath hilum: *cot*, cotyledon; *cot ep*, cotyledonary epidermis; *hi*, hilum; *par*, parenchyma; *p ep*, palisaded epidermis of seed coat; *p ep₁* and *p ep₂*, double layer of palisaded epidermis surrounding hilum; *scl*, porous sclerenchyma; *s ep*, subepidermal cells which are more extensive beneath hilum, forming cushion in which sclerenchyma cells are embedded. (*A* and *C*, redrawn from Tschorch and Oesterle, *Anatomischer Atlas der Pharmakognosie und Nahrungsmittelekunde*, Herm. Tauchnitz; *B*, redrawn from Winton and Winton, *Structure and Composition of Foods*, John Wiley and Sons, Inc.)

have added more or less complete accounts in connection with studies of germination, food storage, and related subjects. In the mature seed, the coat is thin and somewhat brittle, except at the hilum, consisting of three layers, two of which are but one cell in thickness while the third may be several cells thick. (Fig. 174, *A*.) All the layers are a part of the outer integument, since the inner integument is completely resorbed within three or four days after fertilization.

The outermost layer of palisade cells, sometimes referred to as the Malpighian layer, consists of elongated cells which may be from 60 to 100 μ long, and are further characterized by the presence of a narrow light line immediately below the thin cuticle. The cells are thick-walled and the lumen is much broader at the inner end of each cell than at the outer where it is very narrow. The second layer consists of the column cells or osteosclerids, which have a characteristic I-shaped or hour-glass form. They vary from 25 to 40 μ in height and are conspicuous in cross-sectional view. The spongy parenchyma forms the third layer, consisting of 10 to 20 rows of thin-walled cells which are very much compressed and crushed at maturity. At the hilum, two layers of palisade cells are present; and, immediately beneath the slit of the hilum, there is a group of sclerenchymatous cells with reticulate walls which, according to Tschirch and Oesterle, may serve a protective function against the invasion of fungi. The subepidermal layer of column cells is expanded beneath the hilum into a cushion in which the porous sclerenchymatous cells are embedded. (Fig. 174, B.)

According to Pultz (25), the seed coat is the only part of the pea seed that contains starch during the first eight or ten days of growth following fertilization, but it does not at any time contain enough to affect the edibility of the seed. The development of the palisade layer, which may become very hard, is an important factor in tenderness and succulence. Nucellar tissue is absent in the mature seed, and this is also true of the endosperm, which is entirely absorbed by the growing embryo at the end of 11 or 12 days. Prior to this time, the endosperm plays an important part in the nutrition of the developing embryo and contributes to the sweetness and tenderness of the pea until it is more than half grown.

The epidermal cells of the cotyledons are small, rectangular, arranged end to end in rows, and contain protein and fat but no starch. The subepidermal layer consists of a single row of cells containing some starch; and underlying these are numerous large, thin-walled cells which are more loosely arranged with intercellular spaces. The cells of the mesophyll contain starch grains which are variable in shape, being ellipsoid, reniform, or globular with irregular, rounded protuberances.

DEVELOPMENT OF THE SEEDLING. — The development of the pea seedling is hypogaeal. The imbibition of water results in a soft-

ening and wrinkling of the seed coat, followed by a rapid swelling of the cotyledons, and a penetration of the seed coat at the micropylar zone by the tip of the conical hypocotyl. The short hypocotyledonary portion of the axis is, for the most part, root-like; and a few millimeters beneath the cotyledonary node, the epidermis is of the root type producing root hairs. In some cases, the epidermal cells of the first and second internodes are elongated so that they resemble root hairs in appearance.

The cotyledons are diverged at right angles to the seedling axis at an angle of about 120° from each other. Throughout germination, they remain in the testa; but the cotyledonary petioles elongate sufficiently to draw the epicotyledonary portion of the axis out from its original position between the cotyledons. The epicotyl, which has differentiated the first leaves, or trifid bracts, prior to germination, pushes up through the soil, and the differentiation of the true foliage leaves follows. The stem is quadrangular with comparatively short internodes, and the phyllotaxy is distichous. The main shoot may die after a short period of growth, and the development of the plant is continued by branches arising from buds in the axils of the lower bracts or leaves. There are buds in the axils of the cotyledons which usually remain dormant; but, when the epicotyl is severed just above the cotyledons, as is done in connection with some of the experimental work on growth hormones, these may develop rapidly into lateral shoots.

THE PRIMARY ROOT. — The ontogeny of the primary root corresponds to the fourth angiospermous type as described by Janczewski (17), in which growth is accomplished by means of a general meristem that forms a transverse zone extending across the apex of the root. (Fig. 17.) From this generative zone, cell divisions on its distal surface produce the successive layers which form the conical central portion of the calyptra, and divisions of a lateral continuation of this transverse meristem contribute to the marginal portions of the root cap. At a higher level, this lateral meristem functions as a dermatogen and its ultimate divisions produce the epidermis. The proximal face of the transverse meristem gives rise to a massive plerome cylinder, and to a periblem which is several layers in thickness.

In the primary root, the stele is triarch (Fig. 175), rarely tetrapharch, and the protoxylem elements abut the pericycle, which occasionally may be two or three cells in width at those points. The

centripetal differentiation of the metaxylem results in the formation of a solid primary xylem strand; and, early in the ontogeny of the primary phloem, three groups of fibers are differentiated adjacent to the single-layered pericycle. A broad zone of interstitial parenchyma remains between the phloem and the metaxylem regions; and, later in development, a cambium arises in this zone. The cambium is relatively inactive, however; and there is little lateral extension of cambial activity beyond the initial points of origin. Consequently, the production of secondary tissue is limited to a few large xylem vessels; and a small number of phloem elements. (Fig. 176.) The cortex is relatively large, consisting of parenchymatous cells with intercellular spaces at their angles. It is limited outwardly by the epidermis, and the innermost layer differentiates as an endodermis with well-defined Casparyan thickenings.

ROOT NODULES.—The structure of the nodule has been investigated in several species of leguminous plants. These include the work of Pierce (23) on *Medicago denticulata*, Whiting (32) chiefly with *Soja* and *Vigna*, Brenchley and Thornton (1) on *Vicia faba*, Prazmowski (24), who worked with species of *Trifolium*, *Medicago* and *Phaseolus*, and Nemec (21) on *Ornithopus*.

The bacillus causing nodule formation in the pea is *Rhizobium leguminosarum* which, according to Fred, Baldwin and McCoy (9), can induce this reaction in 18 species of legumes. The genus is distinguished from other genera of bacteria by its ability to form nodules on legumes; and, while there seems to be a group specificity, with respect to species of *Rhizobium*, Wilson (33) has pointed out that the question of cross-inoculation groups is still a controversial one.

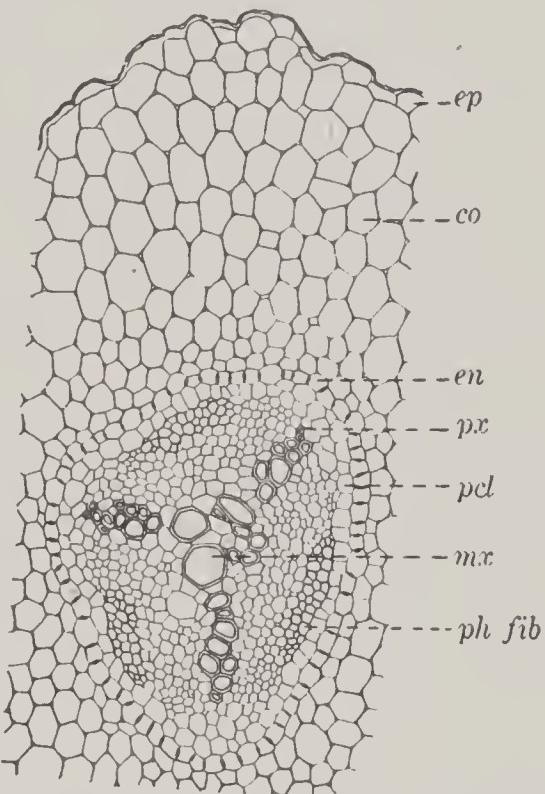


FIG. 175. Transection of sector of young root of pea: *co*, cortex; *en*, endodermis; *ep*, epidermis; *mx*, metaxylem; *pcl*, pericycle; *ph fib*, phloem fibers; *px*, protoxylem.

Invasion of the root by the tubercle bacillus is effected through the root hairs. The bacteria have very little, if any, motility. In nature, they are probably disseminated mainly by the disintegration of the nodules of the host plant, the liberation of the bacteria into the soil and their subsequent spread by such agencies as wind, rain, soil organisms, or by tillage of the soil. When a root

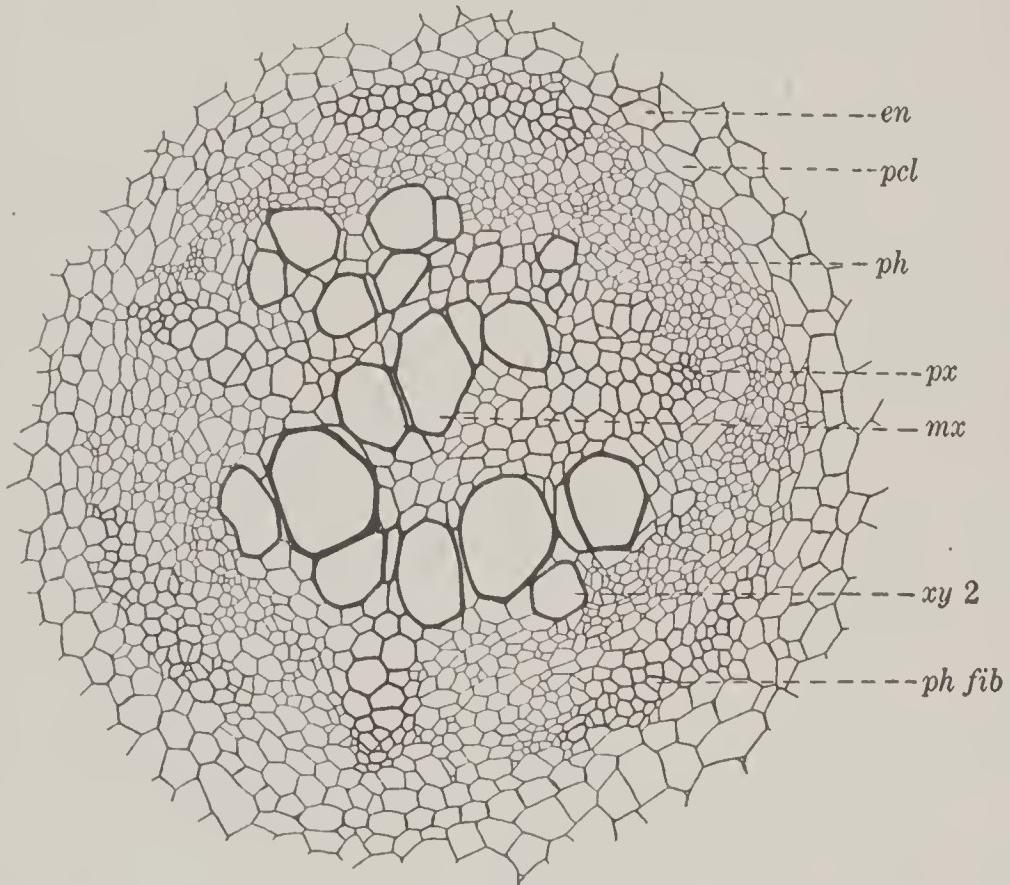


FIG. 176. Transection of stelar portion of nearly mature root: *en*, endodermis; *mx*, metaxylem; *pcl*, pericycle; *ph*, phloem; *ph fib*, phloem fibers; *px*, protoxylem; *xy 2*, secondary xylem.

hair does contact the organisms, they aggregate at its tip and penetrate it by dissolving the cell wall. Thornton and McCoy (26) report that

"there is evidence that . . . a substance is secreted from the roots which assists the entry of the bacteria. Infection of the root hairs is always accompanied by a characteristic curling or deformation of the tip of the hair, which is caused by a filterable secretion of the bacteria. There is some evidence that the root hairs on seedlings are not curled until after the opening of the first true leaves, suggesting that the root secretion also plays a part in producing the curling. The composition of the cell wall in the deformed region appears to be modified and it is perhaps due to this that the organisms can enter at this spot."

"The bacteria penetrate the tissues of the root cortex in the form

of a thread of bacterial zoogloea from which irregular masses of zoogloea grow out within the cells. The thread itself becomes encased in a sheath which is chemically similar to the walls of the host cortical cells and is probably a secretion of the plant. Release of bacteria from the ensheathed infection thread into the host cytoplasm takes place by the formation of blister-like swellings of the sheath which eventually bursts."

The tubercle bacilli multiply rapidly; the thread-like infection strand extends through the length of the hair to its basal portion; and, from that point, continues the invasion through the underlying cortical parenchyma, the endodermis, and finally into the pericycle. As a result of the penetration of this strand, the cells of the pericycle proliferate and form a conical mass of meristematic tissue which in its initial stages resembles the meristem of the primordium of a lateral root. Because of this similarity, the nodule has been regarded as the morphological equivalent of the lateral root, but the resemblance is purely a superficial one.

The dome-like mass of pericyclic tissue pushes out into the cortex, producing a nodular swelling of the root axis at that point. At first, the surrounding epidermal and cortical cells keep pace with the growth of nodular tissue; but later they may become disintegrated as a result of mechanical stretching and abrasion. The central parenchymatous and vascular tissue of the nodule is surrounded by a well-defined endodermal layer, except at the tip, and apical growth of the nodule by means of meristematic activity may proceed for some time. The bacterial tissue occupies the central portion of the nodule, and between this zone and the endodermis are several layers of parenchyma in which two or three vascular strands are differentiated. These abut the protoxylem points of the stele of the root and extend the full length of the nodule to the meristematic zone.

The vascularity of the nodule in *Pisum* is similar in all essential details to that described for *Vicia Faba* by Brenchley and Thornton (1), who state that under conditions of normal nutrition,

"The strands run the full length of the nodule, and merge into the meristematic tissue, the smaller protoplasmic cells being distinguishable for a rather greater distance than are the lignified elements. The strands follow a sinuous course and often branch, and in cross section as many as ten may appear, some of which in reality represent the same strand cut through more than once owing to the curvature. No evidence of anastomosis has been obtained, even in the large nodules

with an abundant vascular supply. Each strand is surrounded by an endodermis which is continuous with that of the root, and which is not evident quite so far as the point at which the tissues merge into the meristem."

There is no cambial activity and secondary growth in the development of the nodule, and the primary growth is limited so that it soon attains full size. Division may take place in the large centrally located cells which contain the bacteria, and intercellular spaces usually are formed. Under normal conditions, the relation of the bacillus to the host plant is a symbiotic one and there is no destruction of the central cells until late in the ontogeny of the host plant; but Nemec, as well as Brenchley and Thornton, points out that under unfavorable conditions there may be a complete disintegration of the central parenchymatous cells, resulting in large intercellular spaces and a general degeneration of the bacteria-containing tissue. Where there is a nutritional deficiency in the soil, such as the absence of boron, there may be a development of incipient nodular tissue in the cortex only, and an absence of pericyclic activity or the development of tracheids in the nodules.

In the symbiotic relationship, the nitrogen bacteria receive carbohydrate material from the host plant and contribute nitrogenous compounds to the host, but the bacteria may become parasitic when the carbohydrate supply to the nodule is suspended. Under these conditions, the bacteria attack and destroy the cytoplasm of the cells in which they are located, ultimately destroying the cell walls as well; and, similarly, a destruction of the nodule tissue by bacteria occurs in old nodules at the end of the growing season.

VASCULAR TRANSITION IN THE AXIS. — The root-stem transition is not completed in the short hypocotyl, but also involves the first three internodes of the stem so that the stele is not an endarch dictyostele until the fourth internode is reached. This situation has been investigated by Dangeard (8), Hérail (15), Tourneux (27), Compton (5), Gourley (11), and the following account is based in part on these reports, supplemented by further investigation of a confirmatory nature.¹

¹ A recent memoir (Muller, C., "La tige feuillée et les cotylédons des Viciées à germination hypogée." *La Cellule* 46: 195-354, 1937) has just been received. This includes a comparative study of the vascular anatomy of the seedlings of five representatives of the tribe Vicieae: *Pisum sativum*, *Vicia sativa*, *V. Faba*, *Lens esculenta*, and *Cicer arietinum*. In this extensive study, Muller describes the vascular anatomy of the seedling in each instance. The author presents a somewhat different interpretation of the relation of the vascular structures than

In the lower hypocotyl, at a level slightly above the triarch root described above (Fig. 175 and Fig. 177, A), definite changes occur in the arrangement of the stelar elements. The xylem is not triarch and the radial primary xylem strand is organized into groups that are tangentially mesarch in their orientation. A central pith is differentiated just below the level of divergence of the cotyledonary traces and the first leaf trace from the hypocotyledonary stele. Tangential bands of metaxylem connect these three potential traces, thus forming with them a ring of vascular tissue which surrounds the medullary parenchyma. (Fig. 177, B.)

Slightly above this point, the three phloem groups are each separated into two distinct phloem strands. (Fig. 177, C.) At succeedingly higher levels, the groups of primary xylem, which are directly continuous with the cotyledonary traces, increase their angular divergence from one another and incline outward. (Fig. 177, D, c-1 and c-2.) Associated with the xylem of each cotyledonary strand are two groups of phloem which originate as branches from the adjacent strands of the root phloems, and the remaining halves of the original phloem groups of the root anastomose outside the xylem of the first leaf trace. (Fig. 177, C, ph l 1.) Each group of cotyledonary phloem is branched, and the resulting strands that lie in the sector between the cotyledons are again divided into several groups, the two median ones anastomosing to form the phloem of the second leaf trace. (Fig. 177, D, l 2.) The two outermost groups of phloem in the intercotyledonary plane, together with small strands of xylem which are diverged from the adjacent metaxylem, continue into the epicotyl as cortical fibro-vascular bundles. (Fig. 177, D, cort fv b.) The remaining phloem groups increase in size and form the four lateral phloem strands of the epicotyl.

At the cotyledonary node, the protoxylem of the second leaf trace is differentiated and lies in the sector between the cotyledonary traces, although Compton notes that the position of the xylem of this trace may vary. (Fig. 177, D, l 2.) In some instances, its initial position is external to the intercotyledonary band of meta-

that given by Gérard, Compton, Gourley and other earlier authors whose work is reviewed. He concludes that the special structure of the central portion of the axis of the first four internodes does not show any relation to the vascular transition of the root and stem, ascribing the characteristic organization of the lower internodes to the peculiar orientation of the confluent.

xylem, and it diverges centripetally until it is continuous with the inner face of this band; in other cases, the trace may occupy this final position from the outset.

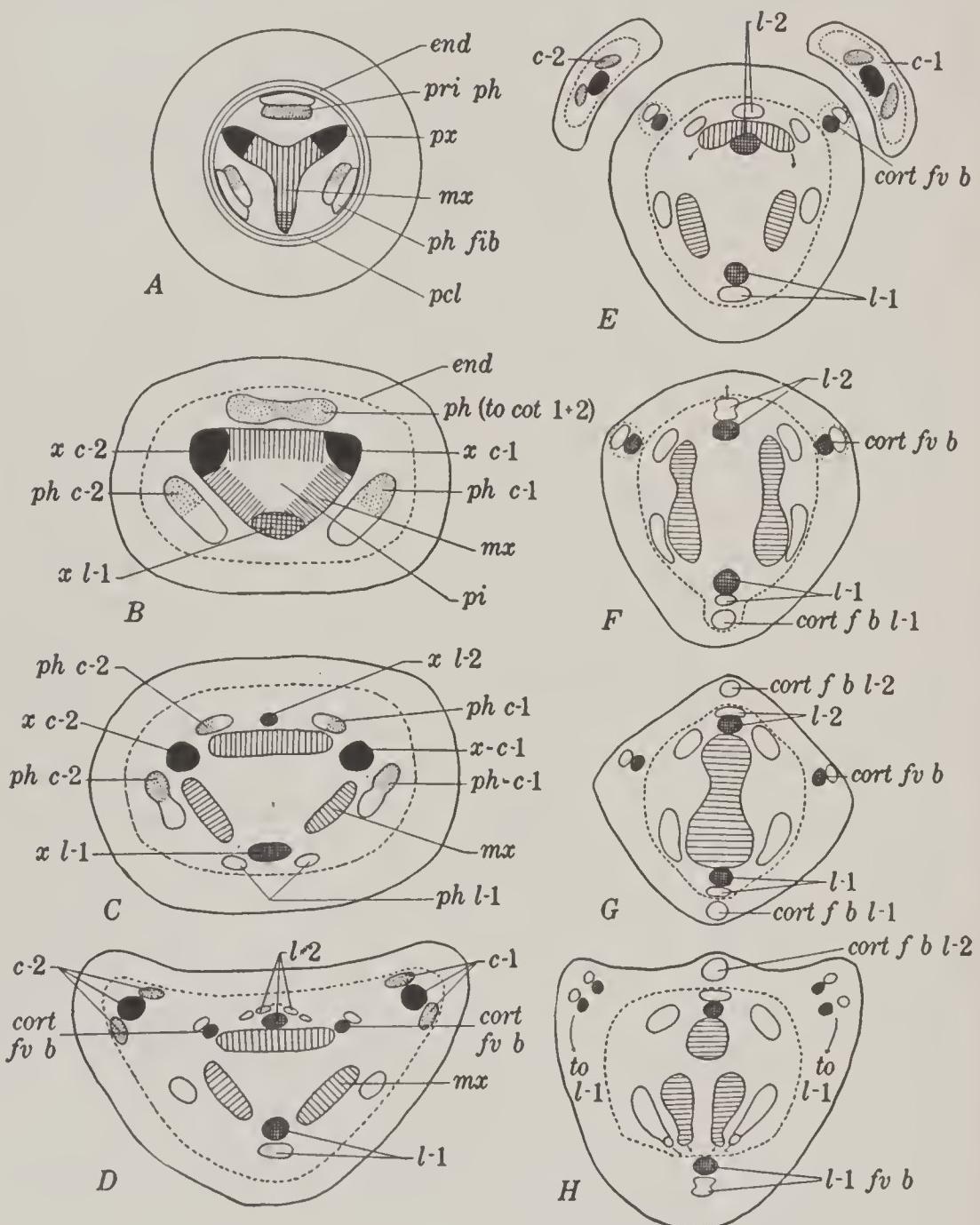


FIG. 177. A-H, diagrams showing vascular transition. A, primary root; B and C, hypostele node; D, cotyledonary node; E, first internode immediately above divergence of cotyledons; F and G, middle and upper regions of first internode; H, second node: $c\cdot 1$ and $c\cdot 2$, cortical fiber bundle to first leaf; $cort f b l\cdot 1$, cortical fiber bundle to second leaf; $cort f v b$, cortical fibrovascular bundle; end , endodermis; $l\cdot 1$, $l\cdot 2$, vascular strands to first and second leaves; $l\cdot 1 fv b$, fibrovascular bundle of first leaf; mx , metaxylem; ph , phloem; $ph c\cdot 1$ and $ph c\cdot 2$, phloem to cotyledons; $ph fib$, phloem fibers; pcl , pericycle; $pri ph$, primary phloem; px , protoxylem; $x c\cdot 1$ and $x c\cdot 2$, xylem to cotyledons; $x l\cdot 1$ and $x l\cdot 2$, xylem to first and second leaves. (B-H adapted after Compton, *Linn. Jour. Bot.*)

At a level just above the point of divergence of the cotyledons, the metaxylem bands undergo further rearrangement, and the band which lies in the intercotyledonary plane on the side of the cotyledonary divergence forms an ellipse. (Fig. 177, E.) This band later divides to form two bundles which anastomose with the lateral groups so that two parallel metaxylem strands are formed. (Fig. 177, F.) In some cases, these anastomose along their inner faces, forming a central zone of metaxylem that occupies the pith region a few millimeters above the cotyledonary node. (Fig. 177, G.)

At this level, the vascular strand, which extends to the first leaf as its median bundle, gives off a fiber strand which is diverged outward into the cortex; and, a short distance above this point, the second leaf trace branches in the same manner. (Fig. 177, F, G.) At the middle of the first internode, as a result of these reorientations, there are four cortical bundles, two of which consist of fibers only, while the other two are fibrovascular. Within the endodermis, there are two polar fibrovascular bundles, a central, dumbbell-shaped zone of metaxylem, and four laterally placed groups of phloem in which fibers are differentiated adjacent to the pericycle. (Fig. 177, G.)

The first trifid bract diverges at the second node, and its median bundle passes out and joins the cortical fiber bundle located on that side of the axis. At the same time, the laterally placed cortical fibrovascular bundles branch, and a lateral bundle from each becomes a lateral vein of the bract. (Fig. 177, H.) Thus, the vascular system of the bract consists of a median and two lateral fibrovascular bundles which later anastomose. The centrally located metaxylem divides along its minor axis into two groups, and the group adjacent to the bract separates longitudinally so that two bundles are produced, which lie centrad to the lateral phloems. (Fig. 177, H.) The two lateral bundles toward the apex of the ellipse give off branches which anastomose to form the median trace of the third leaf. In the third internode, the medullary xylem remaining at the other end of the ellipse divides longitudinally, duplicating the process which took place at the opposite pole in the internode below. As a result of these vascular rearrangements, the fourth internode exhibits a typical stem structure with a central pith and an endarch dictyostele which persists through all higher internodes. (Fig. 178.)

Some variations have been noted with respect to the arrangement of the vascular strands in the epicotyl. In some cases, the medullary xylem does not anastomose to form a solid core; but, after the

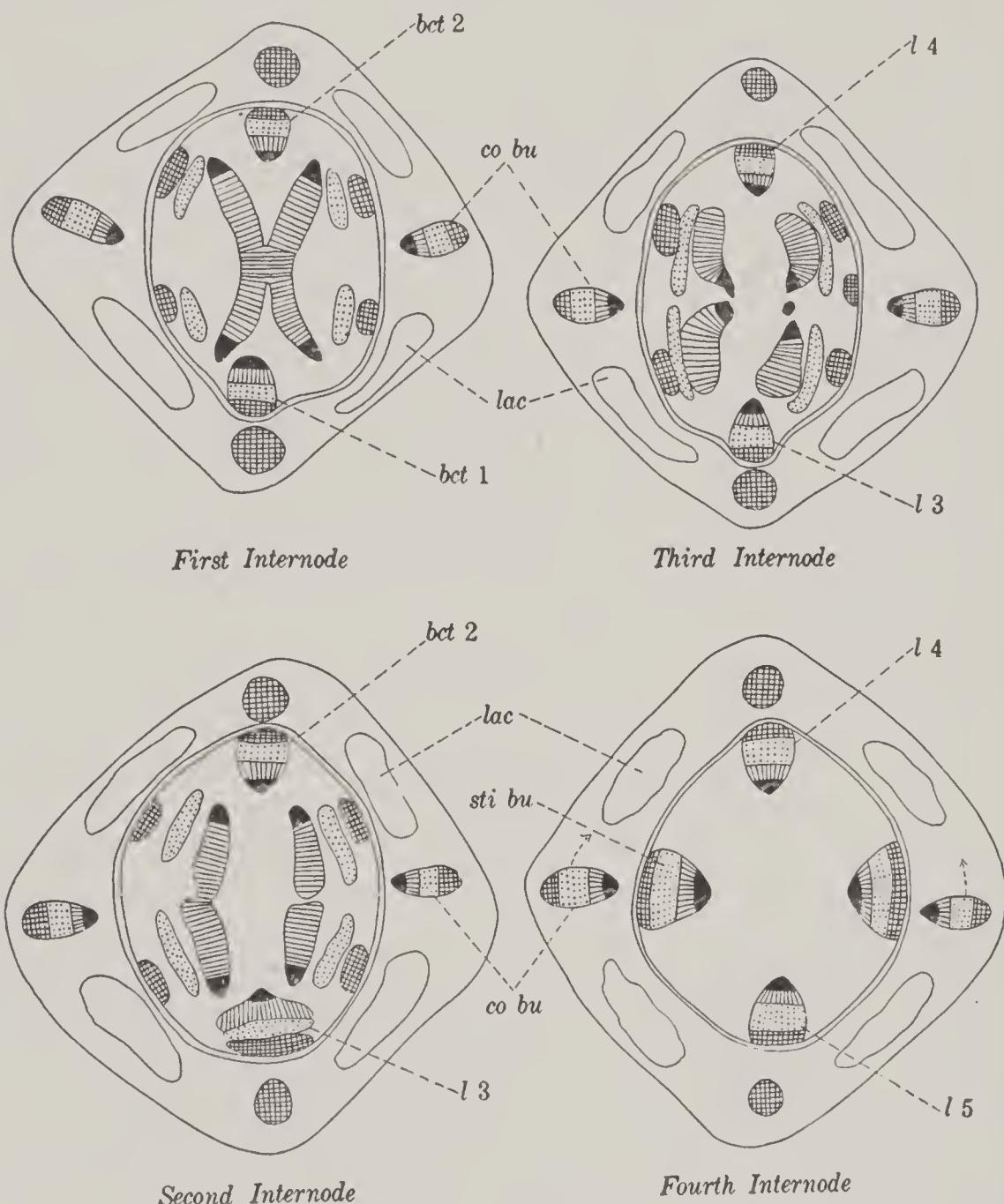


FIG. 178. Diagrammatic transections of first four internodes. Protoxylem is represented in solid black, metaxylem lined, phloem stippled, and phloem and cortical fibers cross-hatched: *bct 1* and *bct 2*, first and second trifid bracts; *co bu*, cortical fibrovascular bundles; *l-3*, *l-4*, *l-5*, traces to foliage leaves; *lac*, lacunae; *sti bu*, stipular bundle.

first tangential fusion into two lateral bands, may break up into eight groups again. In other instances, the lateral phloem groups reunite so that there may be only two or three strands within the endodermis instead of four.

THE STEM. — Since the vascular transition involves the first three internodes of the axis, as well as the hypocotyl, it is desirable to summarize the vascular anatomy of these internodes in order to compare them with the stem pattern which occurs in the fourth internode.

THE FIRST INTERNODE. — The first internode has a wide cortical region limited outwardly by an epidermis which has a thin cuticle and numerous stomata, and inwardly by an endodermis with well-defined Casparyan thickenings. As maturation proceeds, large schizogenous lacunae develop in the cortical parenchyma so that there are usually four such cavities located between the cortical bundles. The cortical bundles consist of two fibrous strands lying in the plane of the polar bundles of the stele and two fibrovascular bundles which lie in a plane at right angles to them. (Fig. 178.)

The stele is bounded by a single-layered pericycle; and abutting this layer are six well-defined groups of phloem fibers, two subtending the polar bundles, the other four being arranged in pairs lateral to the metaxylem. The sieve tubes, companion cells, and phloem parenchyma lie centrad to the groups of phloem fibers. The primary xylem is organized in two distinct regions which differ in the manner in which the proto- and metaxylem are differentiated. The centrally located primary xylem consists of two crescentic bands whose convex surfaces may be in contact at the center of the axis, with the four tips of the crescents directed toward the polar bundles of the stele. (Fig. 179, A.) The development of the primary xylem in this region is exarch, the protoxylem cells constituting the four points of the two bands, while the metaxylem comprises the central primary xylem strand. Parenchyma occupies the space between the protoxylem arms at each pole of the plate. Some variation may occur with respect to the degree of confluence of the two metaxylem bands and there may be a narrow zone of centrally located parenchyma cells between them.

The two polar bundles are endarch and collateral in their orientation, constituting the median bundles of leaf traces. One is the median bundle of the first trifid bract which diverges at the second node, and the other is the median bundle of the second bract-like leaf which arises at the third node. At the upper limits of the first internode, the metaxylem bands described above are somewhat separated laterally, so that there is a narrow central pith parallel to the long axis of the primary xylem strand which is continuous

with the leaf gap resulting from the outward divergence of the polar bundle leading to the trifid bract.

THE SECOND INTERNODE. — The epidermal and cortical regions in the second internode are like those of the first, except that, occasionally, one of the cortical fiber bundles may be divided to form two groups which later converge to form a single strand. In the stele, slightly above the second node, only one polar bundle is completely organized, and at the other pole there is a leaf gap of parenchymatous tissue resulting from the divergence of the median trace to the first trifid bract. (Fig. 179, B.) At a higher level, divergences from the two bands of exarch xylem result in the separation of the central zone of primary xylem into two exarch groups lying adjacent to the leaf gap; and two lateral groups of metaxylem forming the central mass which are separated from each other by a narrow band of parenchyma. Progressive reorientation of the two exarch groups adjacent to the leaf gap results in the formation of a single endarch bundle which becomes the median trace of the third foliage leaf. Near the upper limit of the second internode, which is a relatively short one in most varieties of *Pisum*, the polar bundle supplying the second bract-like leaf is diverged centrifugally through the cortex.

THE THIRD INTERNODE. — The third internode is somewhat more quadrangular in transection than the ones below it, but the cortical organization is identical to that described for internodes one and two. In the stele, each lateral group of phloem fibers may consist of three, rather than two, strands and the laterally oriented bands of xylem are more widely separated by the pith. (Fig. 178.) After the divergence of the polar trace to the second trifid bract at the third node, there is a reorientation of the exarch groups of primary xylem to form a new polar bundle, as described for the opposite pole in the second internode, resulting in the formation of the median bundle for the fourth foliage leaf. The remaining lateral bands of primary xylem may be regarded as tangentially mesarch; that is, the protoxylem of each of the bands is centrally located on its inner face and between flanking groups of metaxylem elements. (Fig. 178 and Fig. 179, C.)

One of the quantitative tests for auxin devised by Went (30) utilizes the third internode of etiolated pea seedlings. When the seedlings are about seven days old, and 10 to 12 cm. in length, the top is cut off 5 mm. below the terminal bud, and the elongated

third internode is bisected longitudinally for about 3 cm. The split halves would curve outward if placed in water because of

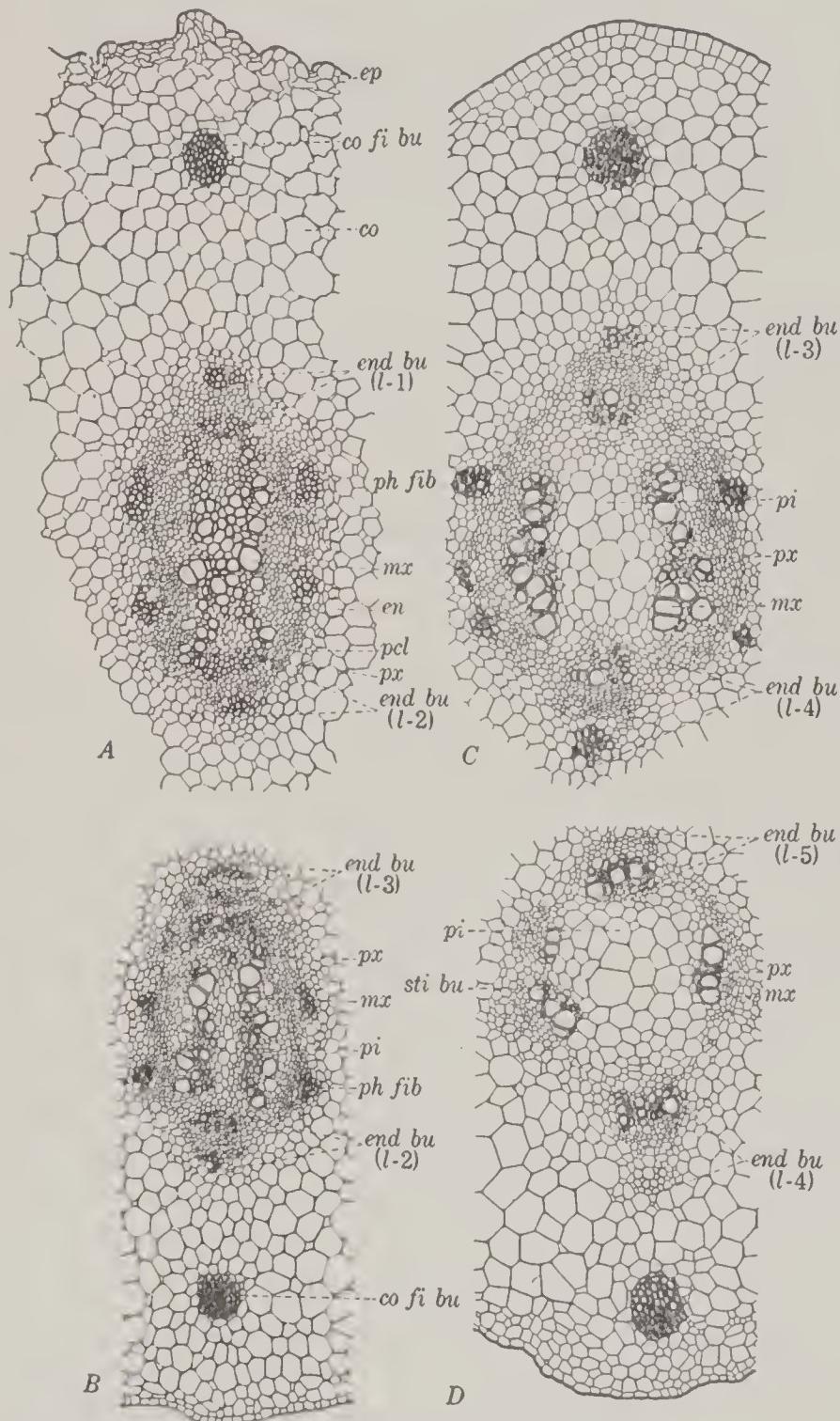


FIG. 179. Transections of axis at various levels to illustrate significant changes in vascular transition. In each figure, the stele and a sector of cortex including one cortical fiber strand are shown. The laterally placed cortical fibrovascular bundles do not appear in the figure. *A*, first internode; *B*, second internode; *C*, third internode; *D*, fourth internode; *co*, cortex; *l-2*, *l-3*, *l-4*, *l-5*, first, second, third, etc., leaves; *mx*, metaxylem; *pcl*, pericycle; *ph fib*, phloem fibers; *pi*, pith; *px*, protoxylem; *sti bu*, stipular bundle.

tissue tension, since the epidermal cells are under tension and the pith cells under pressure; but, when placed in auxin solution, there is an inward curvature of the two halves which can be measured to determine the auxin concentration.

THE FOURTH INTERNODE.—In the fourth internode, a definite stem pattern is laid down, and the transitional situation existing in the lower internodes, in which both exarch and endarch primary xylem groups are found, no longer occurs. The stem is subquadangular and becomes definitely four-sided at internodes above. The endodermis is not as well defined as in lower internodes and in the stele there are two polar bundles which supply the leaves, and, at right angles to them, two bundles which supply the stipules. (Fig. 178 and Fig. 179, *D.*) Higher in the stem the number of vascular bundles in the ring is increased because of the downward divergence of vascular traces from the vegetative and floral axes which develop in the axils of the upper foliage leaves.

Gourley (11) in his study of the course of the cortical fibrovascular bundles showed that they supply the lateral lobes of the trifid bracts, which may be interpreted as homologous to stipules, and the stipules of the vegetative leaves. The polar bundles of the stele provide the chief vascular supply for the central lobe of the trifid bract, and for the lamina of the compound leaf. The cortical fiber bundles which are in the same vertical plane as the polar bundles become a part of the mechanical tissue of the latter when they diverge outward in the nodal region.

The course of the cortical fibrovascular bundles which are located at approximate right angles to the plane of phyllotaxy is as follows: beginning at the cotyledonary node, they diverge from the margins of the vascular bundles which supply the cotyledons. In some instances, two may arise on each side, but only one of these persists. They extend upward in the cortex to the second node, where a branch from each supplies the lateral lobes of the first trifid bract. Within the bract these bundles anastomose with the median stelar bundle so that the bract appears to have a single vascular strand. The main portion of each cortical vascular bundle is continued up through the second internode; and, at the third node, each bundle again branches to supply lateral veins to the lobes of the second bract. The main cortical vascular bundles continue through the third internode; and, at the fourth node, branches from each follow

a spiral course around the stem and enter the stipules at the base of the petiole.

The stipular bundles of the leaf at the fifth node anastomose with bundles of the stele a short distance below the fourth node. These bundles occupy a position in the cortex similar to that of the bundles in the lower internodes, and they can be traced as strands which unite with the vascular bundles of the stele that are located in a plane at right angles to the leaf trace. At the fifth node, a part of each stipular bundle joins with the vascular elements of the blade of the leaf and with them forms its vascular supply. A repetition of this vascular plan occurs at each internode above this point, in this manner providing the vascular supply for each successive set of stipules.

THE UPPER INTERNODES. — Above the fourth internode, the number of bundles increases until there may be twenty or more constituting the vascular cylinder. The upper internodes are subtriangular to quadrangular in outline and the bundles form a dictyostele in which the larger ones are located at the angles of the stem.

The epidermis is well cutinized, and there are numerous stomata surrounded by small guard cells that are about one-half the radial dimension of the adjacent cells. The cortex consists of several layers of chlorenchyma, except outside the larger bundles at the angles of the stem where three or four layers of mechanical tissue may be differentiated. (Fig. 180.) The endodermis is a single layer of large oval parenchymatous cells lying immediately outside the groups of pericyclic fibers that cap the vascular bundles. The fibers are small, thick-walled, and very compactly arranged; but between the fibers and the phloem, there are two or more layers of larger, thin-walled pericyclic cells.

The bundle is collateral with a relatively active fascicular cambium, and there are several layers of secondary phloem and xylem elements formed in the larger bundles. There are few fibers in the phloem as compared with the number found in the transition region. The radial rows of secondary xylem vessels are separated by ray tissue which is thin-walled and parenchymatous.

As the stem matures, the parenchymatous cells of the medullary rays and those abutting the inner face of the bundle become thick-walled, forming a more or less continuous zone of connective tissue. There is some development of a somewhat inactive interfascicular

cambium, and small groups of secondary xylem and phloem are formed between the major bundles of the stele. The large, thin-walled parenchymatous cells of the pith centrad to the connective

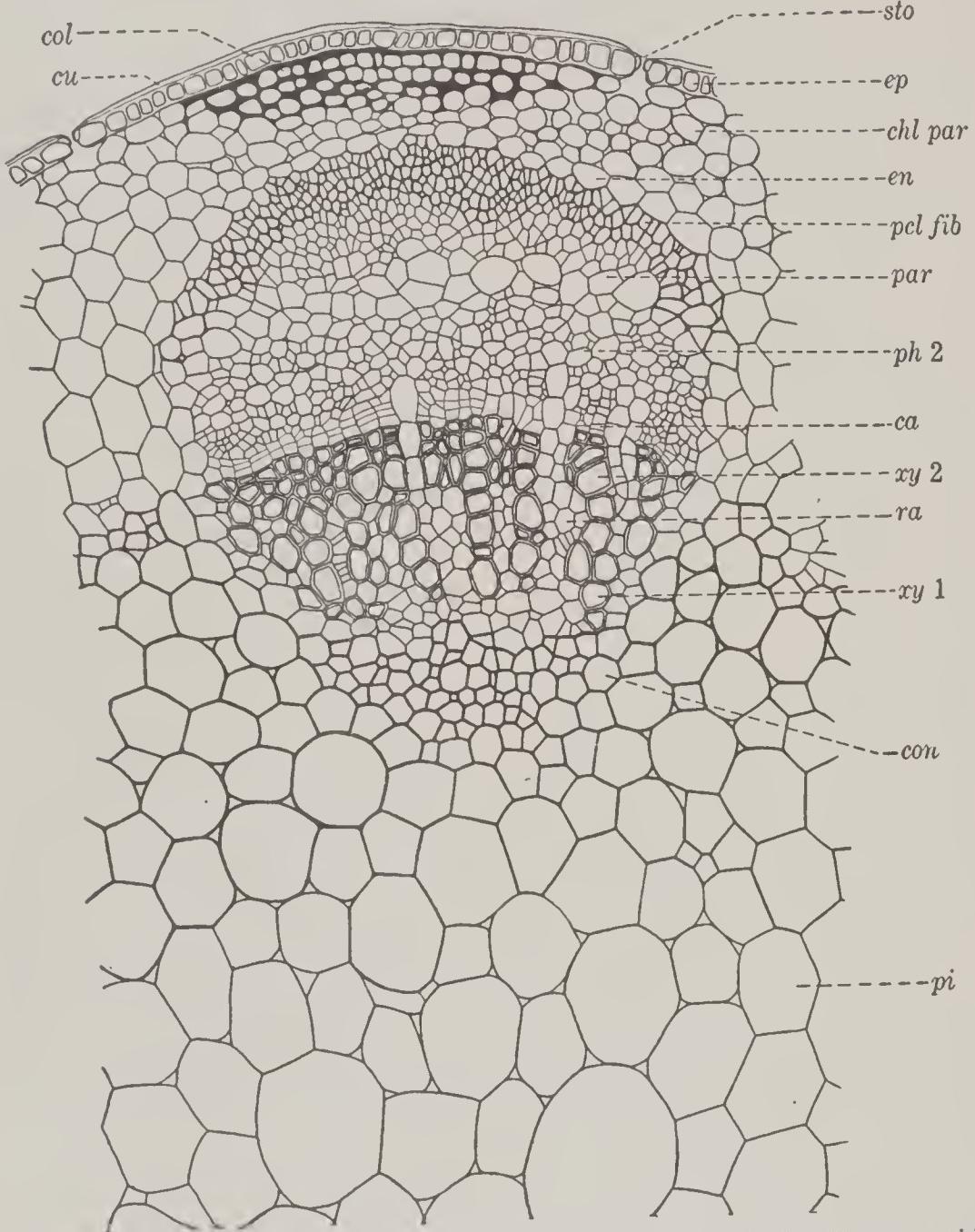


FIG. 180. Transection of sector of upper internode showing vascular bundle: *ca*, cambium; *chl par*, chlorophyll parenchyma; *col*, collenchyma; *con*, connective tissue of pith; *cu*, cortex; *en*, endodermis; *ep*, epidermis; *par*, parenchyma of pericycle; *pcl fib*, pericyclic fibers; *ph 2*, secondary phloem; *pi*, pith; *ra*, ray; *sto*, stoma; *xy 1*, primary xylem; *xy 2*, secondary xylem.

tissue usually disintegrate so that the mature stem is commonly hollow.

ANATOMY OF THE LEAF — THE BLADE. — The blades of the paired leaflets are very thin, and the mesophyll, except in the region of

the principal veins, does not exceed more than six or eight cells in thickness. (Fig. 181, A.) Both of the somewhat papillate epidermal surfaces are thinly cutinized, and the cells are sinuous in outline, except for those lying above the veins, which are elongated parallel to the long axis of the leaf.

Stomata are approximately twice as numerous on the lower surface as the upper, Holman and Robbins (16) reporting counts of 216 and 101 per sq. mm. respectively. They are formed by the interposition of a wall which cuts off one of the lobed portions of an epidermal cell to form the stomatal mother cell. Subsequent division of this mother cell produces the two guard cells, which are somewhat depressed below the surface of the adjacent epidermal cells.

The palisade layer consists of a single row of slender cells and comprises about one-third of the thickness of the mesophyll. The cells are loosely organized so that numerous intercellular spaces occur between adjacent groups and this is also true of the spongy tissue, which consists of from four to six layers of parenchymatous cells. (Fig. 181, A.) The principal veins are collateral, and the abaxial surface of the leaflet is ridged along the line of the midvein because of the development of a strand of mechanical tissue which parallels it. Supporting tissue is also developed on the adaxial face of the large bundles and there may be a few phloem fibers at the abaxial margin of the phloem region of the bundle. The larger veins have a cambium, and a limited amount of secondary vascular tissue is formed, the

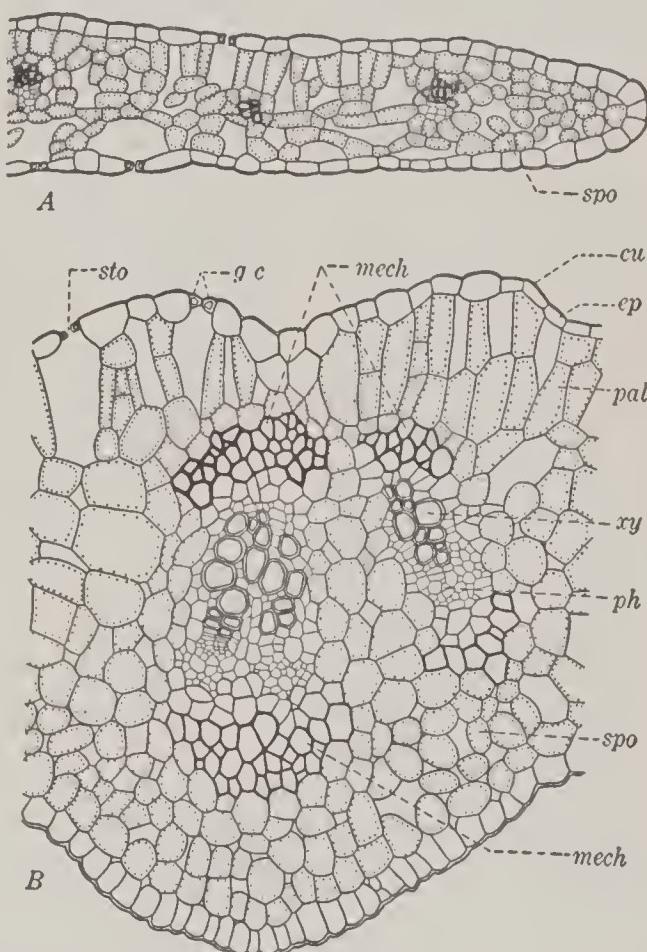


FIG. 181. A, transection of marginal portion of blade of leaflet; B, transection through midvein: cu, cuticle; ep, epidermis; g c, guard cells; mech, mechanical tissue; pal, palisade; ph, phloem; spo, sponge cells; sto, stoma; xy, xylem.

smaller ones consist of a few primary xylem and phloem elements, and the ultimate veinlets end blindly in the mesophyll. (Fig. 181, B.)

THE PETIOLE. — The petiole is terete to subtriangular and contains three main bundles. The largest one is located on the abaxial side of the petiole, the other two lie toward the adaxial surface, occupying points about equidistant from the abaxial bundle; and, between the main bundles, two or more smaller vascular strands may occur. (Fig. 182, A.) The epidermis resembles that of the

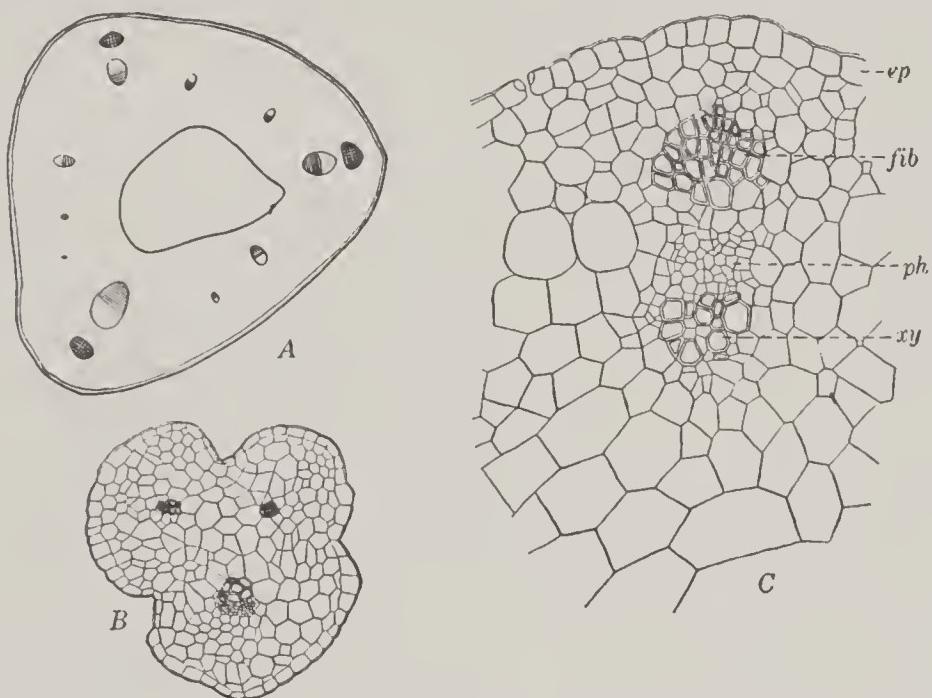


FIG. 182. *A*, diagrammatic transection of petiole showing arrangement of bundles. Cross-hatched portions indicate fibers; stippled portions, phloem; lined regions, xylem. *B*, transection of leaf tendril showing arrangement of bundles; *C*, detail of a sector of petiole showing bundle: *ep*, epidermis; *fib*, fibers; *ph*, phloem; *xy*, xylem.

blade with a thin cuticle and stomata similar to those described for that organ. The subepidermal region consists of several layers of chlorenchyma, and the central portion is made up of large thin-walled parenchymatous cells which ultimately disintegrate so that the mature petiole is usually hollow. The main bundles resemble those of the stem. (Fig. 182, C.)

THE TENDRIL. — The leaf tendril is subtriangular in transection, its adaxial and lateral faces being somewhat grooved. Like the petiole, it has three main bundles, the abaxial one which frequently has a subtending cap of mechanical tissue being larger than the two adaxial bundles. (Fig. 182, B.) The remainder of the tissue is chlorenchymatous.

FLORAL DEVELOPMENT. — Floral development in the Legumino-sae has been investigated for several genera, including the work of Goebel (10) on *Phaseolus* and other legumes; Grégoire (12) on *Lathyrus*; Bugnon (3) on *Lathyrus*, *Trifolium* and *Lupinus*; Westgate, Coe, and others (31) on *Trifolium*; Coe and Martin (4) on *Melilotus*; and Guard (13) on *Soja*. The floral development in these genera is in agreement with that of *Pisum*, the only important difference of opinion being in regard to the character of the car-

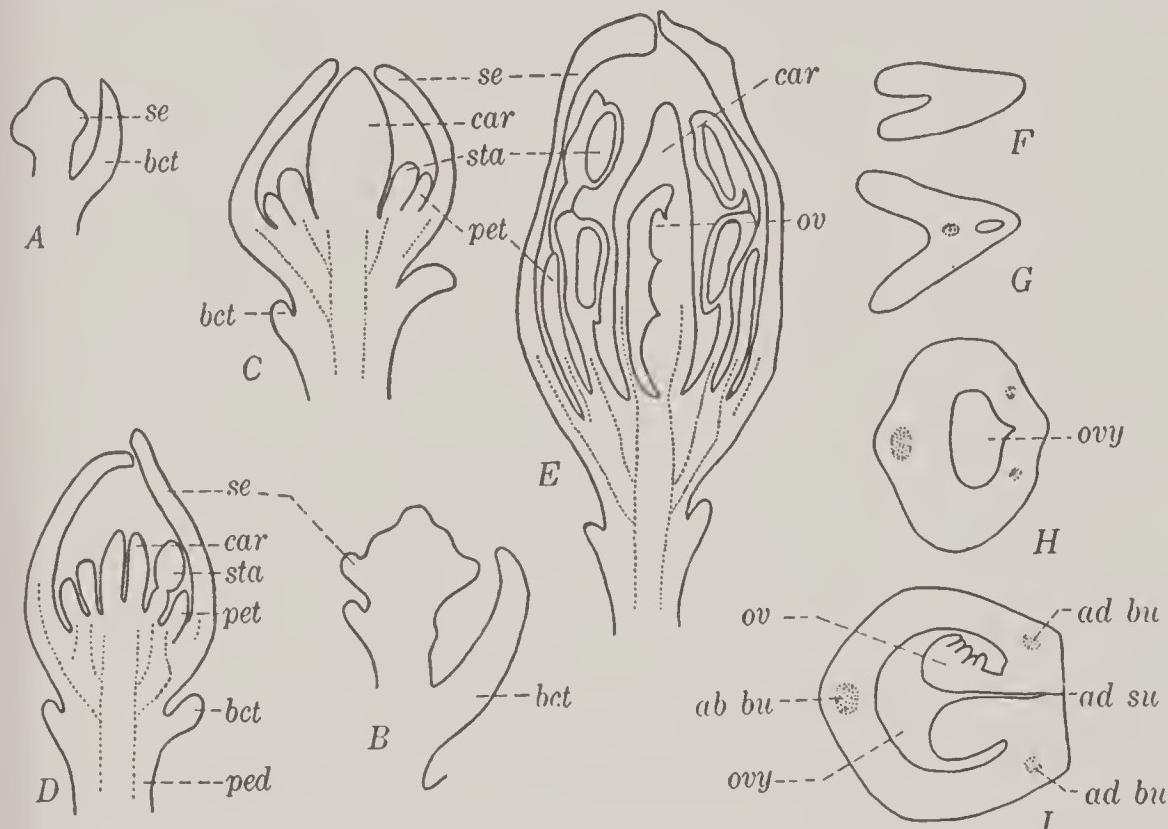


FIG. 183. A-E, diagrammatic longisections of flower bud showing stages in development; F-I, diagrammatic transections of carpel in E, showing vascular anatomy and origin of ovules; *ab bu*, abaxial bundle; *ad bu*, adaxial bundle; *ad su*, adaxial suture; *bct*, bract; *car*, carpel; *ov*, ovule; *ovy*, ovary; *ped*, pedicel; *pet*, petal; *se*, sepal; *sta*, stamen.

pillary development in which the interpretation of Grégoire is not in complete accord with the findings of other investigators.

The flower primordium first appears as a knob-like growing point of meristematic tissue in the axil of a bract. (Fig. 183, A.) The sepals, petals, outer cycle of stamens, inner cycle of stamens, and carpel then appear in the order named, but the subsequent development and maturation of the floral parts does not follow this succession. The first of the five sepal primordia arises from the growing point on the abaxial side, followed by the development of the two lateral lobes of the calyx, and, finally, the two adaxial lobes. (Fig. 183, B.) Shortly after the initiation of the pri-

mordia of the sepals, zonal growth takes place at their bases, and the continued growth of this zone and the tips results in a cylindrical tube with five acuminate lobes at its outer margin. This forms a protective covering over the growing point and other floral parts. (Fig. 183, *E.*)

As the growth of the calyx proceeds, the five petal primordia arise from the growing point alternate with the sepal lobes, the two primordia which form the keel of the corolla being formed first, followed by those of the two lateral wings and the standard. The primordia of the keel are at first distinct structures; as growth proceeds, their adjacent edges become more or less completely united along the abaxial margin of the keel; and, at maturity, they form a hood-like structure which partially surrounds the stamens and carpel. (Fig. 184, *F, G, H.*) Although the petal primordia are the second cycle of organs to be differentiated, they grow very slowly at first, remaining small during the early development of the stamens.

In the mature flower, the stamens are diadelphous and appear to be arranged in one whorl in which nine stamens are "united" by their filaments, while the tenth, adaxial stamen is free. This is due to the perigynous development of the flower, in which there is non-divergence of the basal portions of the stamen primordia, and the early ontogeny indicates that the flower is actually pentacyclic with two whorls of stamens, each consisting of five primordia. (Fig. 184, *H.*) The development of two cycles of stamens as noted above has also been reported for *Trifolium*, *Melilotus*, *Phaseolus* and other legumes.

As a result of the growth of the tissue basal to the whorls of stamen primordia, the bi-cyclic character of the androecium is soon obscured, and nine of the stamens develop with a common basal collar of non-diverged tissue, leaving the tenth stamen free. (Fig. 184, *G.*) This stamen is a member of the inner whorl, and the elongation of its free filament maintains the anther at the same level as those of the other members of the whorl. The maturation of the filaments and anthers of the outer whorl is more rapid than that of the inner, and the outer stamens produce mature pollen grains earlier. (Fig. 183, *E.*)

Immediately following the differentiation of the inner cycle of stamen primordia, the carpel primordium is differentiated, and grows so rapidly that it soon becomes larger than any of the other

primordia except the enclosing sepals. (Fig. 183, C, D.) It arises as an open crescentic structure with its abaxial surface directed toward the keel of the flower. (Fig. 183, G, H.) Thus, the young carpel develops as an open sporophyll whose edges later coalesce, becoming united so intimately that the original suture can only be detected with difficulty in the mature ovary, and may be completely obliterated. (Fig. 183, I.) This type of development has been described by all the investigators cited above with the exception of Grégoire who has stated that in *Lathyrus* there is no distinct line between the carpillary margins at any time. It seems doubtful, in the light of other work, that this can be the case; and Bugnon, studying the same genus, has found it to be in agreement with the development reported above.

VASCULAR ANATOMY OF THE FLOWER.—Moore (19, 20) has investigated the vascular anatomy of the flower in a number of the papilionaceous legumes, dividing the species studied into two major series based upon the number of cycles of traces which supply the perianth and the androecium. He places *Pisum* in the "dihiate" series, under the *Lathyrus* type in which two cycles of traces supply the perianth and androecium, and "the gaps of the perianth traces extend into the departing stamen traces making the stamen traces appear double in origin." Moore's account of this type agrees in its major details with that given below, the chief difference being in the ultimate branching of the traces supplying the petals.

In a transection of the pedicel of a very young flower slightly below the receptacle, the vascular tissue forms a partially dissected siphonostele in which several distinct vascular strands may be differentiated in the provascular ring. (Fig. 184, A.) Slightly above this level and below the floral node from which the calyx primordia arise, 10 perianth traces diverge obliquely from the vascular ring. (Fig. 184, B.) This is followed by the divergence of the stamen traces from the vascular ring, and three primary carpillary traces are finally differentiated from it. (Fig. 184, C, D.) The branching of the perianth traces occurs just below the nodes from which the petals diverge, and alternate perianth bundles incline inward, forming the principal veins of the five petals. At this point of inward differentiation, each petal trace gives off two lateral branches which continue upward and become the right and left lateral calyx bundles of the adjacent sepals. The median bun-

dle of each sepal lobe is one of the unbranched perianth bundles, and branches from the petal traces form the main laterals. (Fig. 184, E.) Additional branching of the midvein and laterals results in the formation of a number of small veins which extend throughout the undiverged portion of the calyx. (Fig. 184, F, G, H.) Finally, each ultimate calyx lobe is supplied with three principal bundles, each petal and stamen has one main bundle, and the vas-

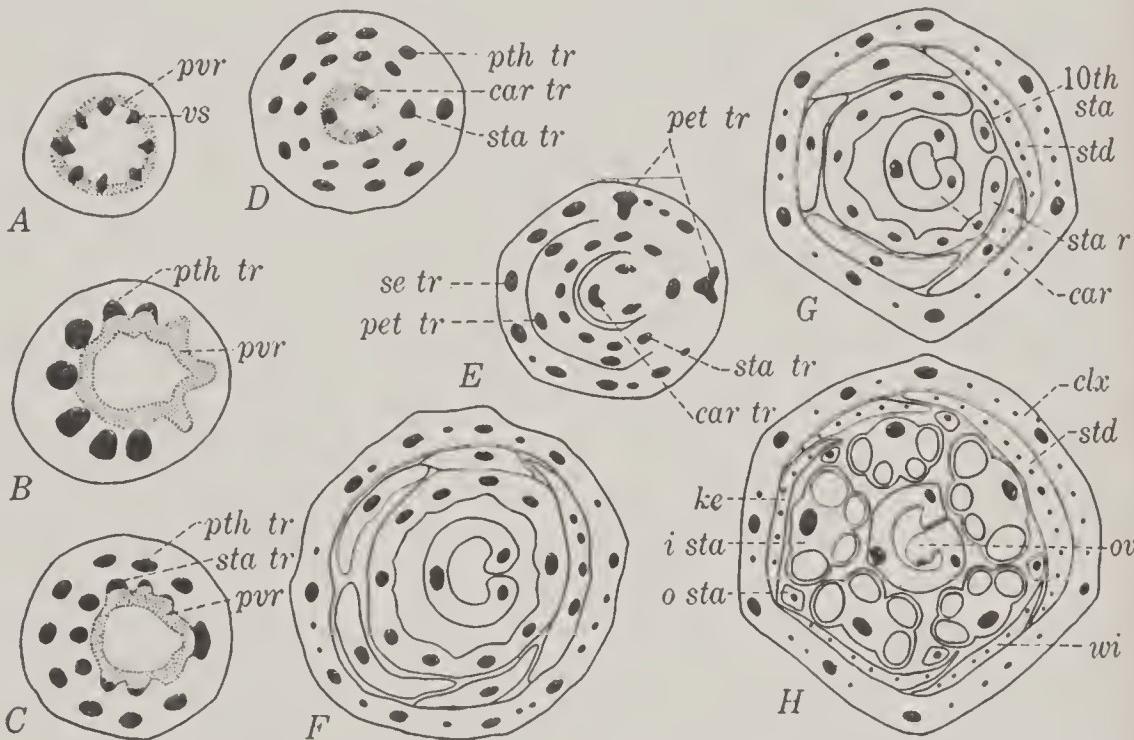


FIG. 184. A-H, diagrammatic transections of flower bud from pedicel upward showing arrangement of vascular traces and floral parts: *car*, carpel; *car tr*, carpellary trace; *clx*, calyx tube; *i sta*, inner stamen; *ke*, keel; *o sta*, filament of outer stamen; *ov*, ovule; *pet tr*, petal trace; *pth tr*, perianth trace; *pvr*, provascular ring; *se tr*, sepal trace; *sta r*, staminal ring; *sta tr*, staminal trace; *std*, standard; *vs*, vascular strand; *wi*, wing.

cular system of the carpel consists of a large abaxial and two smaller adaxial bundles. (Fig. 183, I.)

MICROSPOROGENESIS. — Sporogenesis in the garden pea has been investigated by Cooper (7), who used two horticultural varieties, Little Marvel and Asgrow's Pride. The microspore mother cells have larger nuclei than the tapetal cells which ultimately become binucleate. The somatic number of chromosomes is fourteen and seven pairs are present at diakinesis. Following the second meiotic division, each microspore mother cell has four nuclei. The division spindles persist for a time and cell plates are formed, after which the walls of the four microspores are deposited. The pollen grains are soon released from the microspore mother cell wall; and, subsequently, the walls of the former thicken except for two germ pores.

The nucleus of the microspore divides to form a tube cell and a smaller generative cell, the former disintegrating early so that it may disappear completely by the time of pollination. The generative nucleus divides during the growth of the pollen tube, and the two microgametes which are surrounded by a narrow layer of cytoplasm are separated from the cytoplasm of the tube by a thin membrane.

DEVELOPMENT OF THE OVULE AND MEGASPOROGENESIS. — As the young carpel develops, the ovules arise on the adaxial margins of the carpel along two parietal placentae. (Fig. 183, I.) At this time, the adaxial suture is still visible; but in the later development of the carpel, it becomes less and less distinct. At maturity, the carpillary margins are intimately fused and the ovules appear to be arranged in a single row. This appearance is further emphasized by the formation of an abaxial suture and the development of parenchymatous ray tissue which bisects the large abaxial bundle. The suture becomes more and more pronounced and finally constitutes one of the lines of dehiscence in the mature fruit.

The ovule first appears as a dome-shaped primordium of nucellar tissue and at its base two integuments arise in close succession. The outer integument precedes the inner one and by its rapid growth soon encloses the latter. As the integuments are differentiated around the nucellus, the ovule curves toward the stylar end of the carpel and gradually becomes campylotropous.

In megasporogenesis, a hypodermal cell at the apex of the ovule becomes the archesporial cell, and divides to form a primary parietal and a primary sporogenous cell. The latter functions as the megaspore mother cell, enlarging and developing a finely vacuolated cytoplasm preceding diakinesis. Cooper (7) noted several cases in which two or even three sporogenous cells developed in the ovule.

Four megasporocytes result from the meiotic divisions, and the one nearest the chalaza is functional, enlarging and elongating prior to further division. The usual sequence follows, three successive nuclear divisions producing an eight-celled megagametophyte. (Fig. 185.) Three of the nuclei remain at the chalazal end and become the antipodal nuclei, three form the megagamete and synergids toward the micropyle, and the other two serve as the polar nuclei uniting at about the time of fertilization. The mature megagametophyte is elongated and curved, eight nucleate, and seven celled.

EMBRYOGENY. — Studies of embryogeny in the Leguminosae indicate that there are many variations in the details of embryo development. Guignard (14) has pointed out that these are due in part to significant differences in the character of the suspensor and the shape of the proembryo in the early stages of embryogeny. However, Martin (18), working with *Trifolium* (three species), *Medicago*, and *Vicia*, found that all five were alike in the development of the integument of the ovule, in the production of four megasporangia, and in the rapid destruction of the nucellar tissue in

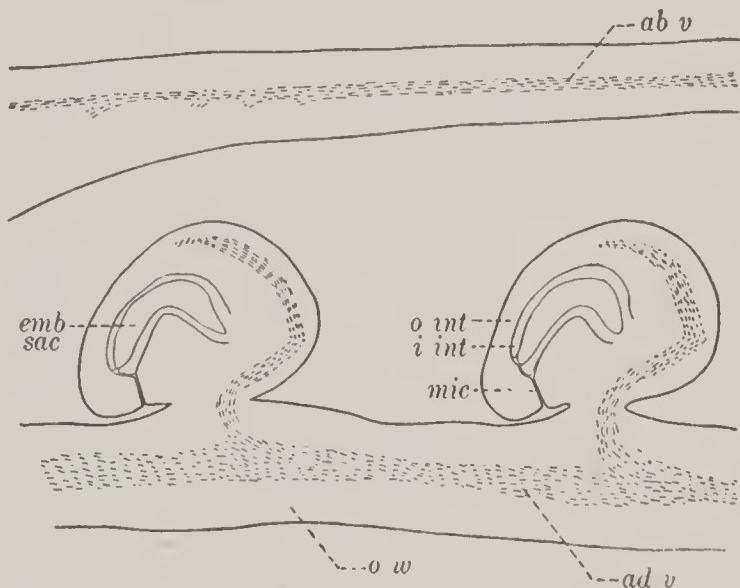


FIG. 185. Longisection of portion of carpel showing orientation of developing ovules: *ab v*, abaxial vein; *ad v*, adaxial vein; *emb sac*, embryo sac; *i int*, inner integument; *mic*, micropyle; *o int*, outer integument; *o w*, ovary wall.

embryogeny, indicating that certain groups of legumes may be very similar in their developmental behavior.

According to Cooper (6), fertilization occurs in the late bud stage about 12 to 24 hours before the open flower stage. Following fertilization, the first division of the zygote is transverse, and at this two-celled stage the endosperm may be two or four nucleate. This occurs in the open flower stage and by the time the flower has withered, the proembryo is four-celled, the division of the basal cell being longitudinal. The true embryo develops from the apical cell of the four-celled proembryo while the two basal cells form much elongated, multinucleate structures which, with the derivatives of the middle cell, constitute the suspensor. The middle cell also divides longitudinally, and the daughter cells likewise become multinucleate, much enlarged and globular. These four multinucleate cells disintegrate as the cotyledons develop.

Pultz (25) in his study of the deposition of starch in the seeds of *Pisum* has followed the embryogeny from early stages to maturity. Twenty-four hours after pollination, when the embryo is just beginning to develop, there is an abundant accumulation of starch which is strictly localized in the cells of the inner integument and in those of the outer integument at the chalaza near the end of the embryo sac. (Fig. 186, A.) At the end of thirty-six hours, the young embryo is developing in the embryo sac near its micropylar end, and by this time the endosperm occupies a peripheral position.

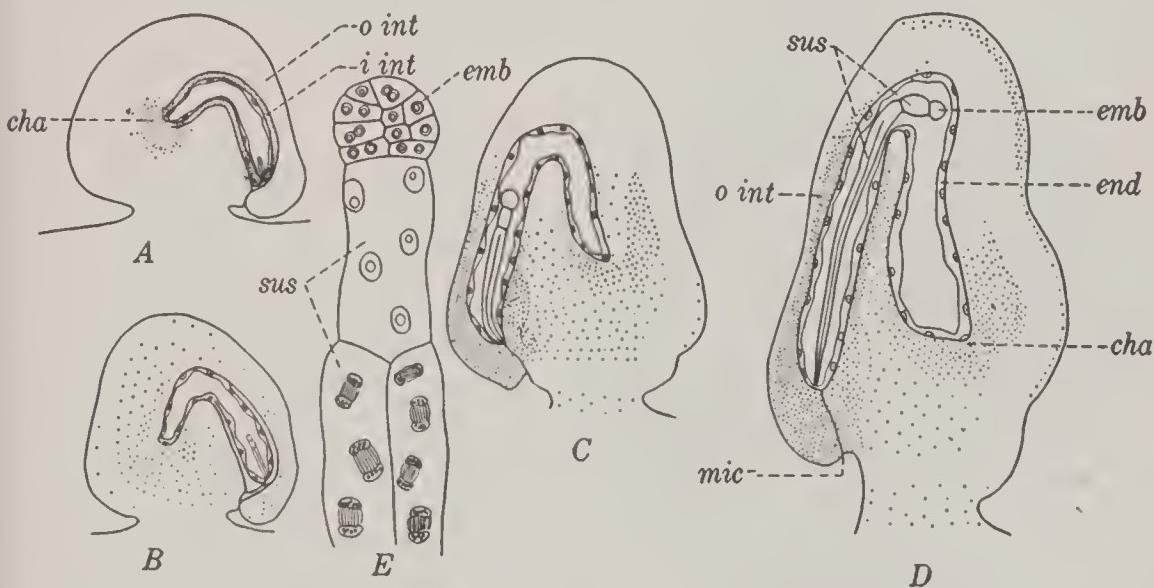


FIG. 186. A-D, stages in development of ovule showing progressive deposition of starch, represented by dots. A, ovule, 24 hours after pollination; B, same, 48 hours after pollination in which digestion of inner integument is beginning and a more general distribution of starch is evident; C, young seed three days after pollination, showing complete digestion of inner integument and presence of starch in outer integument; D, young seed four and one-half days after pollination, showing change in position of embryo and increased deposition of starch; E, diagrammatic drawing of young embryo and suspensor: cha, chalaza; emb, embryo; end, endosperm; i int, inner integument; mic, micropyle; o int, outer integument; sus, suspensor. (Figures A-D after Pultz; E after Guignard, *Ann. Sci. Nat.*)

Both the embryo and endosperm are devoid of starch at this stage, but there is an increase in the starch in the inner and outer integuments. (Fig. 187.)

Between two and three days after pollination, continued growth of the embryo results in the complete digestion of the nucellar tissue and the beginning of digestion of the inner integument and the starch which it contained. (Fig. 186, B.) At this stage, the suspensor begins to elongate; and the embryo is pushed toward the curved portion of the embryo sac where it ultimately completes its development. Three to four days following pollination, the inner integument is completely resorbed and the embryo sac is enlarged

and lined with a peripheral layer of endosperm. The starch is still restricted to the outer integument, but it is increased in amount near the micropyle and at the chalaza. (Fig. 186, C.) At about five days, the embryo occupies a position in the curved portion of the embryo sac, and the endosperm constitutes a considerable proportion of the seed, since the embryo sac is enlarged and the embryo is relatively small. (Fig. 186, D.) The endosperm nuclei are peripherally located, the central cavity of the embryo sac contains a watery cytoplasm; and, although starch is present in increased amounts, it is still restricted to the outer integument.



FIG. 187. Ovule thirty-six hours after pollination, showing development of embryo sac and peripheral position of endosperm. Dark areas indicate regions of starch deposition. (Photomicrograph by Pultz.)

matic regions of the cotyledons; and when the seeds are eight or nine days old, starch appears in the middle region of the cotyledons and at the cotyledonary plate. The peripheral cells on the abaxial surface and tips of the cotyledons continue to divide and contain little or no starch, as is also the case in the hypocotyl and epicotyl.

The developing embryo occupies a small part of the embryo sac, the remainder being filled with a more or less watery, sweet-tasting endosperm. Starch is not present in the endosperm at this or at any other time during its development. The cotyledons continue to grow actively by means of a peripheral band of meristematic cells, and this is followed by a progressive deposition of starch which explains the greater amounts in the middle of the cotyledons

About six days after pollination, the embryo differentiates cotyledons which enlarge as a result of an increase in the number and size of cells, divisions taking place somewhat more rapidly near the periphery. Later, this meristematic condition is restricted to the tip and outer surface of each cotyledon, and the cells at the center and toward the adaxial surface enlarge and cease dividing. It is at this stage that starch deposition is initiated in the non-meristematic

and at the cotyledonary plate, than along the edges of the cotyledon which are practically without starch, at least in the meristematic zone.

The endosperm never becomes definitely cellular, although temporary walls may form around the nuclei adjacent to the embryo as described for *Phaseolus* by Brown (2). By the time the seed is eleven to twelve days old, the endosperm has been entirely digested. The mature seed consists of the embryo and the seed coat, the latter being developed from the outer integument only, the inner integument being completely digested during the growth of the embryo.

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CHAPTER XIII

LINACEAE

LINUM USITATISSIMUM

THE flax family is not a large one, and common flax is the only member of economic importance, except for a few species that are grown for decorative purposes. In addition to commercial fiber, the plant produces oil which is extracted from the seed, the residue being pressed into cakes that are used as food for livestock.

There is evidence that flax was grown during the Stone Age, and its cultivation and preparation for fiber constituted one of the earliest textile industries. It has been cultivated so long that it is not now known in its wild state, although an annual form grows as an escape in the vicinity of the Persian Gulf and the Caspian and Black seas. The first cultivated form was a biennial type with small, narrow leaves, *Linum angustifolium* Huds.; but the annual or common flax, *Linum usitatissimum* L., has been grown in Mesopotamia for at least 4000 years.

The major portion of the crop is produced in Russia, but fiber of the finest quality is grown in Belgium and Holland. Other countries which raise flax commercially include: Austria, Hungary, France, Ireland; and, to a lesser degree, Germany, Italy, Rumania, and Japan. In Argentina, India, and the United States, the crop is grown chiefly for the linseed oil, rather than for the fiber, and is known as seed-flax. This is produced in North and South Dakota, Wyoming, and Montana, where the climate is too dry for fiber flax. Robinson (19) has pointed out, however, that it is possible to grow fiber flax of excellent quality in the United States, and this is being done in the Willamette Valley in Oregon, as well as the Puget Sound region in Washington, where cool, moist weather obtains from March to June, followed by a warm, dry climate in July.

All the varieties used in the United States are regarded as belonging to one species, *L. usitatissimum*; and, although much of the seed is imported from Europe and Russia, that of several vari-

eties, including the widely grown Bison, is produced in this country. For high quality fiber, most growers regard seed from the Netherlands and Belgium, which has been derived from Russian strains, as most desirable.

GENERAL MORPHOLOGY

THE Root. — The root system consists of a slender tap root 3 or 4 feet in length with lateral branches that arise mainly from its upper limits. Ten Eyck (24), in describing it, states that

"flax has a different system of rooting from that of wheat or oats. Its roots do not go so deep . . . but it makes a much greater fibrous root growth in the upper two feet of the soil. Each plant sends down a single, small taproot, which gives off many small side roots or branches, and these in turn give off numerous fibrous roots or feeders. The upper branches soon curve downward along with the main root which grows rapidly slender and thread-like, until it can scarcely be distinguished from its branches. . . . By its intricate system of rooting flax occupies the soil very completely."

Arny and Johnson (3) studied the progressive development of the Winona variety in Minnesota. They found that the tap root reached a depth of approximately 3 feet, when the plants were beginning to bloom and the stems were 2 feet tall, there being a lateral spread of about a foot. The shallow main lateral roots grew horizontally for about 6 inches, then turned sharply downward, and ultimately equaled the main tap root in length. When the plant was in full bloom, after nearly two months' growth, the tap root was about $3\frac{1}{2}$ feet long; and another 6 inches was added in the ensuing five weeks which brought it to full maturity.

THE SHOOT. — The stem is slender and erect, branching at some point above the middle, usually nearer the top, to form the few-flowered inflorescence which may be a panicle, corymb, or cyme (Fig. 188.) In flax grown for fiber, the length of the stalk from the soil surface to the lowest branches of the inflorescence is an important factor in determining quality, as only the unbranched portion of the axis has commercial value since the fiber in the branches is broken in the processes of fiber preparation.

The simple leaves are linear to lanceolate, sessile, entire, and without stipules. The leaf arrangement is variable, but the basal leaves are commonly in alternate pairs, while those above the

fourth node are spirally arranged. (Fig. 189.) Tognini (25) reported the phyllotaxy as $\frac{2}{5}$, but noted that there were frequent exceptions to this plan even on one plant. Crooks (7), working with the Bison variety, occasionally found three leaves in a whorl



FIG. 188. Panicles of Bison flax showing flowers and arrangement of leaves.
(Courtesy Bureau Plant Industry.)

at one of the lower nodes and observed cases in which leaves at the sixth, seventh, or eighth nodes were bilobed. (Fig. 199, A.) In some of these, the leaf was broad and cleft nearly to the base of the lamina; in others, it was narrow with a very small cleft at the apex. Ontogenetic studies indicate that such double leaves are the result of the non-divergence in varying degree of two leaf primordia.

THE FLOWER. — The flowers are terminal and blue or white in commercial varieties, the more common blue-flowered types frequently having a streak of dark blue in the throat of the corolla. The white-blossomed types require 7 to 10 days longer for blooming

and are grown very little in the United States since they produce a relatively coarse fiber. The flowers are hypogynous and tetracyclic with five sepals, five petals, five stamens, and a compound pistil of five carpels in a radially symmetrical arrangement. (Fig. 190, A-F.) The persistent sepals are much imbricated in the bud and are unequal in size, the two outermost ones being smaller than the other three, the third sepal intermediate in size, and the two innermost ones the largest. The blade of the sepal is oval, acuminate and glabrous, except for the margins which may be scarious, and the tip is ciliated. The ephemeral petals are wedge-shaped, about twice the length of the sepals, and their margins overlap one another in either a right- or left-handed spiral. In most instances, the flowers open in early morning and the petals begin to fall at about nine or ten o'clock when the sun becomes hot; but, if it



FIG. 189. — Habit of flax plant showing character of stem and inflorescence. (Photograph by Copson.)

is cloudy, the corolla may remain in place throughout the day.

The androecium is slightly monodelphous at the base; and, on the margin of the undiverged staminal ring, there are usually five tooth-like staminodia which alternate with the filaments of the five fertile stamens. These are small processes, not exceeding a millimeter in length; but Tammes (22) has reported cases in which varying degrees of development were found, some even

producing anthers containing pollen. The anthers and pollen in both the blue and white varieties of fiber flax are blue; but the pollen is sometimes yellow in the oil flaxes, especially in the Indian varieties; and the anther walls may be yellow or white. On the outer side and at the base of each filament, there is a nectary

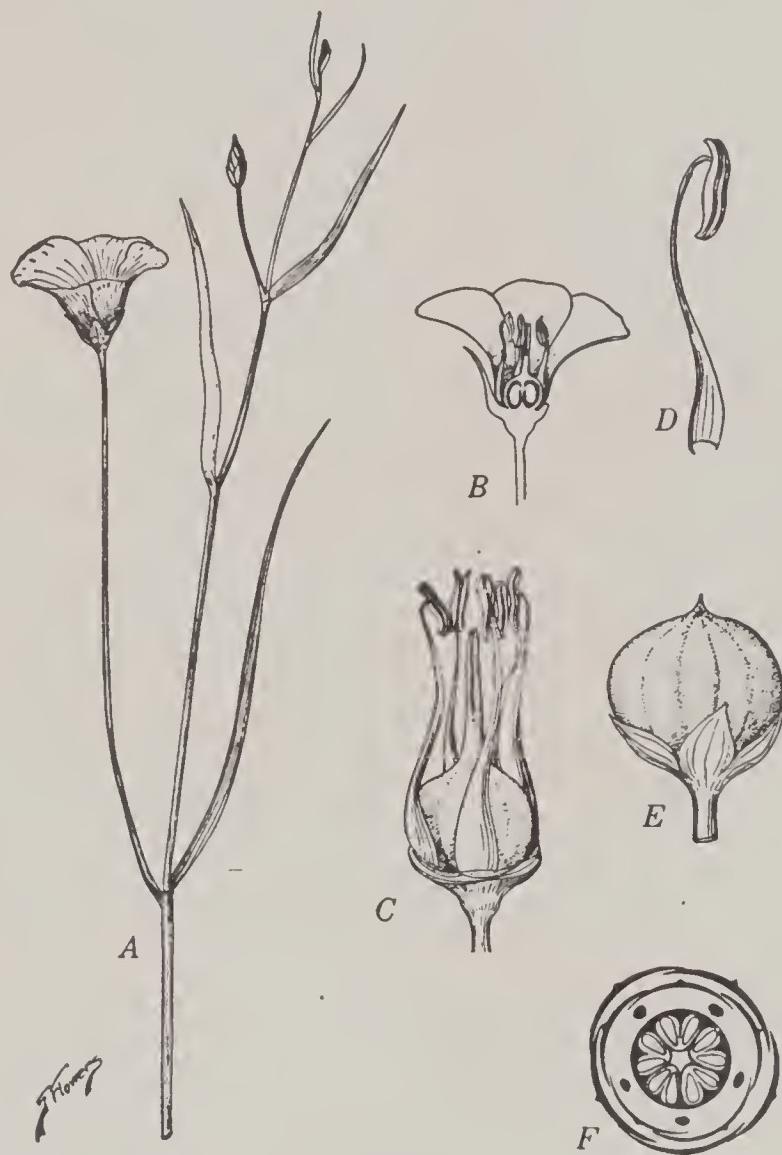


FIG. 190. A, inflorescence; B, longitudinal view of flower with portion of perianth removed; C, stamens and pistil with perianth removed; D, stamen; E, mature fruit; F, floral diagram.

at the lower end of a longitudinal groove. The anthers are introrse and when the flowers close toward noon, the filaments are bent inward so that the anthers contact the stigmatic surfaces, resulting in self-pollination. The pistil has five distinct styles and stigmas, but the carpels are undivided at their bases. The ovary is five-loculed, although it often looks ten-loculed because of the formation of false septa which develop on a line with the dorsal suture,

growing centripetally until they partially or completely divide each locule. The septa are non-ciliate in some forms and pilose in others, the latter condition existing in most non-dehiscent types.

THE FRUIT. — The fruit is a spherical or egg-shaped capsule 10 to 12 mm. in diameter and 8 to 15 mm. in height. It is dry at maturity and the partial dehiscence is septicidal, but each locule may also separate into two parts along the line of the dorsal septum so that the ripe fruit seems to be ten-parted. Tammes (22) reports a variation with respect to dehiscence in flax, it being the general condition in wild species and in a form of cultivated flax, *L. usitatissimum crepitans*, Böningh., which is still grown in some regions of the Ukraine. In other cultivated forms, the capsule is either non-dehiscent, or only slightly so at the apex of the fruit, and the seeds cannot escape. Two anatropous ovules arise from axillary placentae toward the summit of each locule so that they appear to be suspended. (Fig. 192, A.)

THE SEED. — The somewhat beaked, oval seeds are flattened or lens-shaped in transection and variable in size, being designated as small or large in commercial practice. In general, the seed of oil flax is the larger, averaging about 5 to 6 mm. in length and 2.5 to 3.5 mm. in diameter, while that of fiber flax approximates 3 to 5 mm. and 2 to 2.5 mm. respectively. The smooth surface is highly polished and the seed coat may vary in color from white to various shades of yellow or brown, some being reported as variegated.

DEVELOPMENT OF THE SEEDLING. — The germination of the seed is rapid at temperatures of 65–75° F., and the primary tap root emerges in one or two days, constituting the main axis of the root system. The seedling emerges above the ground level in four or five days and the hypocotyl elongates at its basal point, curving until it takes the shape of an inverted U. (Fig. 191.) It pulls the cotyledons and seed coats above the ground, and in about five days, the hypocotyl straightens and the remains of the seed coats are shed. After a period of general growth, there is a zonal elongation of the hypocotyl which is initiated at the ground level and extends progressively upward to the cotyledonary plate until growth in length ceases at the end of 15 to 20 days. The first lateral roots appear in five to six days, usually emerging within 3 cm. of the soil surface, and most of the subsequent ones originate

along the upper 8 cm. of the primary root. When the cotyledons are liberated from the seed coats, they separate and expand for several days prior to the elongation of the epicotyl, which differentiates very slowly at first, appearing as a compact bud with several small leaves at the end of 12 to 15 days.

After the seedlings are about an inch above the ground, they grow slowly for two or three weeks and then there is rapid increase

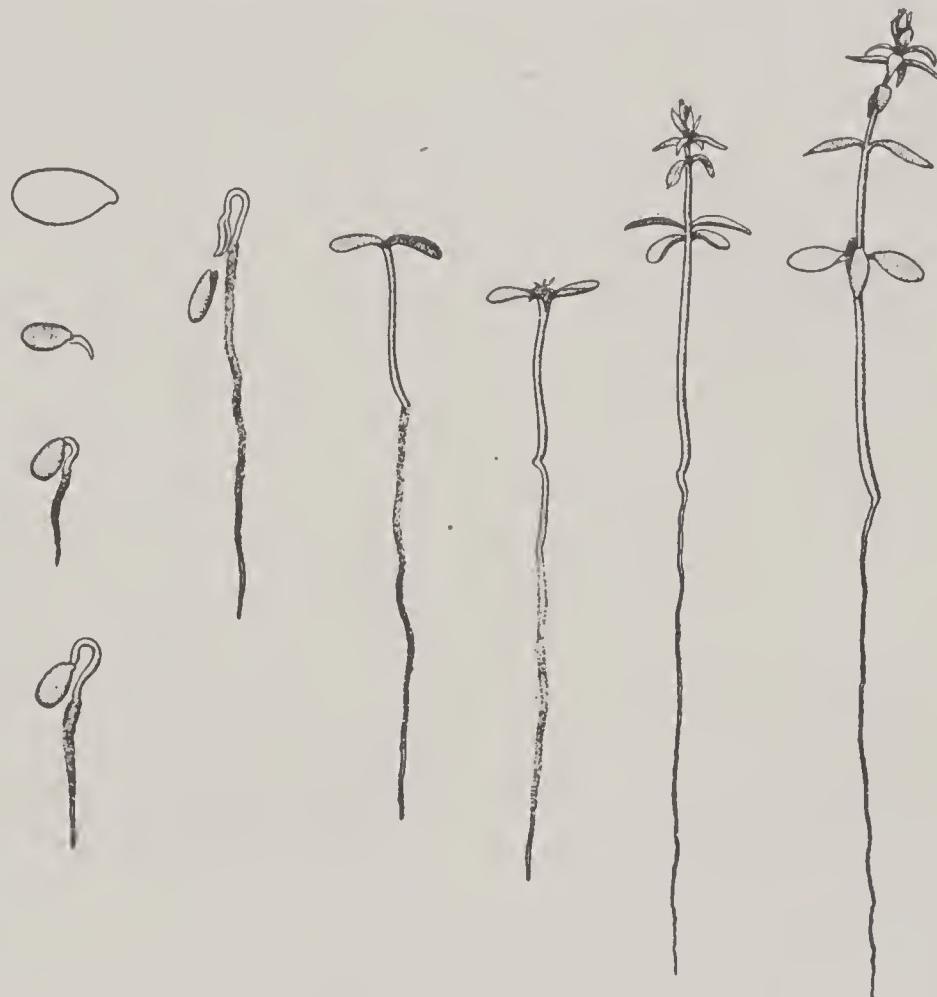


FIG. 191. The seed and stages in development of seedling.

in height which continues until the time of blossoming if conditions are favorable. The first internode always remains short, not exceeding 1 mm. in length at maturity, the second internode is longer than the others, attaining a length of about 15 mm., and the remaining ones vary from 5 to 10 mm.

ANATOMY

ANATOMY OF THE SEED. — The mature seed coat consists of several distinct layers. The outer one is made up of cells which are polygonal in surface view and rectangular in longisection.

They are covered by a finely granular cuticle; and, as the cells develop, stratified layers of material are laid down against the thick outer walls until they nearly fill the cell cavities with a

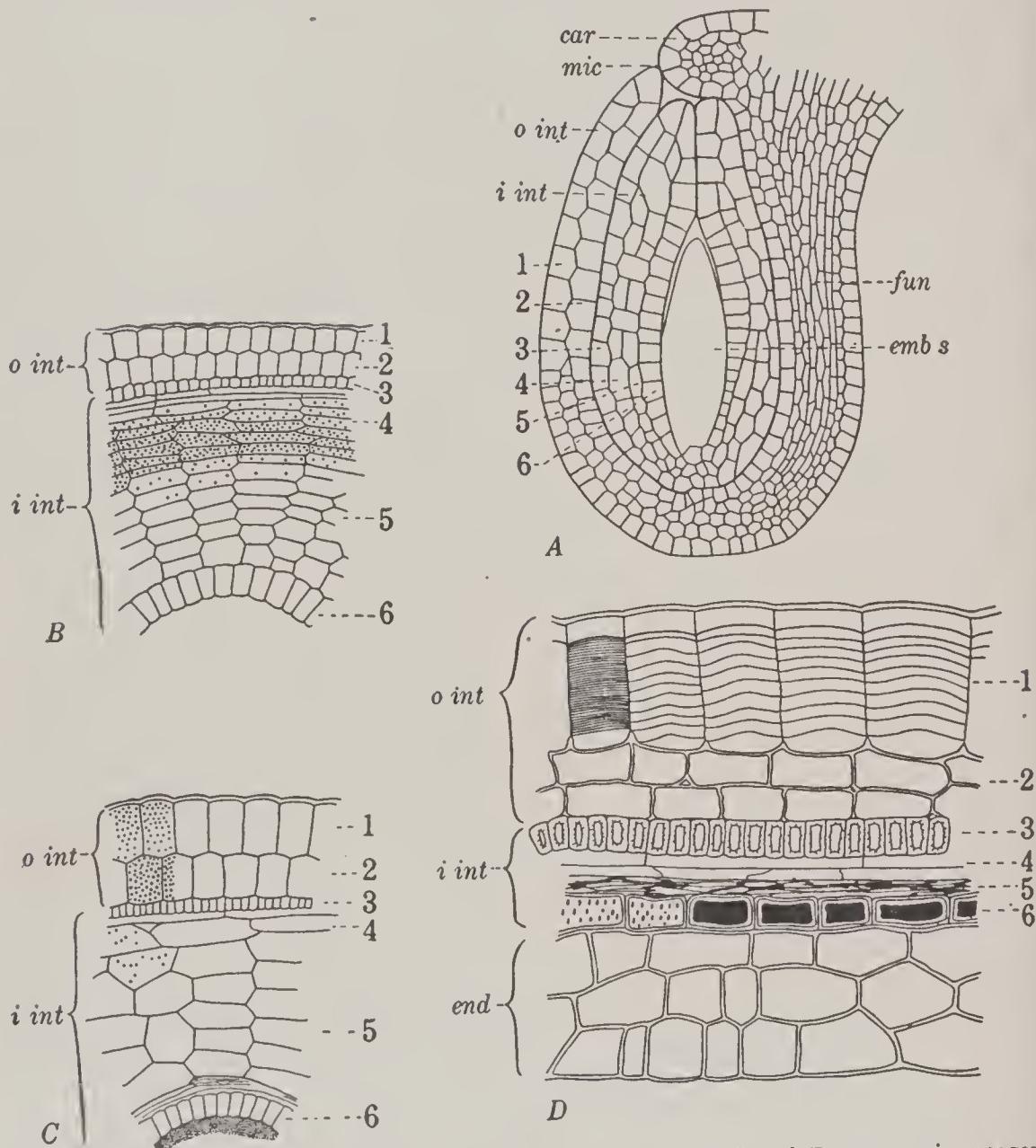


FIG. 192. A, median longisection of anatropous ovule; B, C, and D, progressive stages in development of seed coats. The numbers 1-6 represent corresponding cell layers or their derivatives in the four figures: car, caruncle; emb s, outline of embryo sac; end, endosperm; fun, funiculus; i int, inner integument; mic, micropyle; o int, outer integument. (Redrawn after Tschirch and Oesterle, *Anatomischer Atlas der Pharmakognosie und Nahrungsmittelekunde*, Herm. Tauchnitz.)

mucilaginous substance that is related to the medicinal properties of the seed. (Fig. 192, D.)

Haberlandt (9) has described the structure and behavior of this layer when water is gradually imbibed. Each cell is separated from those adjacent by a thin, sharply defined middle lamella

which is limited externally in the cutinized outer wall. As the secondary layers gradually absorb water, their stratification becomes very evident and they begin to swell. The middle lamellae are relatively inelastic; and, as a result of the pressure exerted by the swelling layers against the comparatively tough cutinized outer wall, they give way and the outer walls are lifted up and fissured by the prismatic masses of swollen mucilage.

Underlying the epidermis are one or two layers of "round cells" with well-developed intercellular spaces, which are so called because of the circular appearance of the cell cavities in surface view. The third layer consists of longitudinally oriented fiber cells which are thick-walled and porous. According to Winton (28), their length may vary considerably, ranging up to $250\ \mu$ with radial dimensions that greatly exceed their breadth. The fourth and fifth zones are made up of several layers of very thin-walled, colorless "cross cells" which are so named because their long axes are oriented at right angles to the fiber cells. Tschirch and Oesterle (26) found that the cells of this zone contain large deposits of starch; but, as the seed develops, this is utilized and the cells become crushed and more or less obliterated.

The uniseriate pigment layer is the innermost one of the seed coat, and is made up of cells that are square or polygonal with thick porous walls and contents which determine the color of the seed. The straight embryo has a short hypocotyl and two long fleshy cotyledons that are thicker than the surrounding endosperm. This varies in thickness, consisting of from two to six layers of parenchymatous cells which are thicker walled than those of the cotyledons and contain aleurone grains and fat.

EMBRYOGENY. — The early stages in the development of the embryo of the Linaceae have been described by Souèges (20), who used *Linum catharticum* L. as a type form. Following fertilization, the first division of the zygote occurs in a transverse plane producing an apical and a basal cell, and subsequent transverse divisions of these two cells result in the formation of a linear row of four cells, *l*, *l'*, *m* and *ci*. (Fig. 193, 2-6.) Of this linear series, the apical cell, *l*, always divides in a vertical plane; and the basal cell, *ci*, always divides transversely. The division of cell *l'* is usually either longitudinal or transverse (occasionally oblique); and cell *m* may divide transversely or longitudinally. (Fig. 193, 7-21.)

Because of the variation in the divisions of the two median cells of the linear tetrad and the consequent variation in the orientation of the derivative cells, three distinct types of eight-celled proembryos occur. The most common one is an octant which has seven linear layers of cells; but other possibilities include ones with six or with five layers. (Fig. 193, 13, 15.) All later stages in the embryonic development can be referred to one of these three types, the derivatives of the more common seven-layered type are

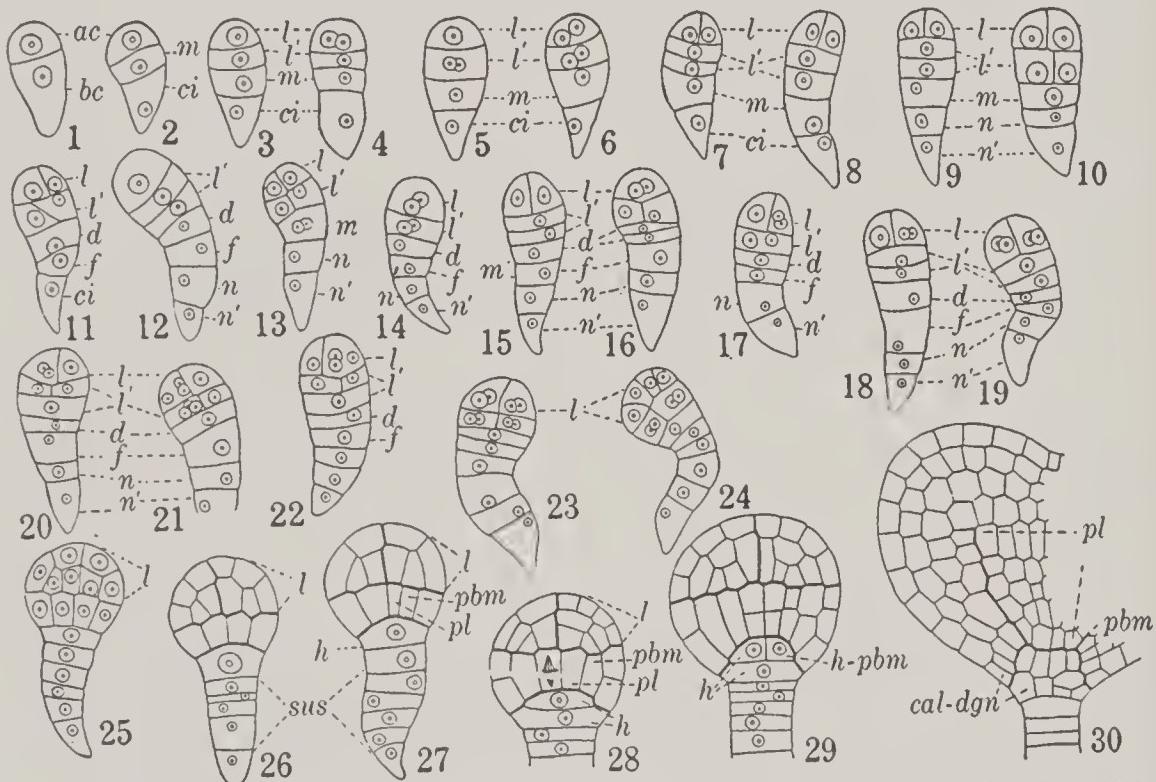


FIG. 193. Early stages in development of embryo of *Linum catharticum* L.: *ac* and *bc*, apical and basal cells of the proembryo; *m* and *ci*, cells derived from basal cell; *l* and *l'*, cells derived from apical cell; *n* and *n'*, cells derived from *ci*; *d* and *f*, cells derived from *m*: *cal-dgn*, calyptrogen-dermatogen; *h*, hypophysis; *pbm*, periblem; *pl*, plerome; *sus*, suspensor. (Redrawn and adapted from Souèges, *Compt. Rend. Acad. Sci.*)

shown in Figure 193, 19, 20, 22, and those of the six-layered type in Figure 193, 18, 21.

In the subsequent development of the embryo, the cell *l*, or the upper daughter cell derived from it, undergoes periclinal division, and further development of the resultant cells leads to the differentiation of the cotyledonary portion of the embryo. The behavior of the cells *l'* and *m* of the original tetrad varies with the type of eight-celled proembryo; but in the most common case (the seven-layered proembryo) the cell *l'* divides into two superposed cells, the upper one producing the hypocotyl, while the lower one divides again transversely, forming two cells. The upper of these

two cells becomes the hypophysis and the lower one contributes to the development of the suspensor. In the case of the six-layered octant, derivatives of the cell l' form the hypocotyl; and the upper daughter cell, d , derived from the cell m , produces the hypophysis after one or two subsequent transverse segmentations while the lower daughter cell, f , enters into the structure of the suspensor. In the least frequent case, in which the octant consists of five layers (Fig. 193, 13), the layer l' produces the hypocotyl and the layer m , the hypophysis. This divides transversely to form two cells which enter into the development of the two outer histogens of the growing point of the root tip. The upper cell contributes initials to the periblem, while the lower one becomes a part of the calyptrogen-dermatogen layer that produces the root cap terminally and the epidermis laterally. (Fig. 193, 29-30.)

THE PRIMARY ROOT. — The primary root has a diarch protostele with two rather large groups of primary phloem flanking the primary xylem strand. (Fig. 197, A.) Tognini (25) has reported a special case in which seedlings differentiated three cotyledons, and the six downwardly diverging cotyledonary traces were united in pairs in the lower hypocotyl so that the primary root had a triarch stele.

There are three to five elements in each protoxylem group, and the metaxylem vessels are successively larger toward the center. The pericycle and endodermis are single-layered and the Caspary strips of the latter are laid down on the radial and end walls before the metaxylem is mature. The cortical cells are isodiametric with large intercellular spaces, except for the compact hypodermal layer in which the cells are somewhat radially elongated and resemble the epidermal cells. The cortex persists for some time and when disintegration occurs, as a result of secondary thickening, it begins in a midregion between endodermis and hypodermis.

The ontogeny of the primary root has been investigated by Janczewski (13), who used it to illustrate a special variation in his third type of angiospermous roots in which the plerome and periblem are sharply defined, and are covered by a common initial layer which gives rise to the epidermis and root cap. In most roots with this type of development, the periblem consists of a single layer at its apical point and becomes wider laterally by subsequent periclinal divisions; but, in flax, the apical portion of the periblem consists of two initial layers. In his studies of the devel-

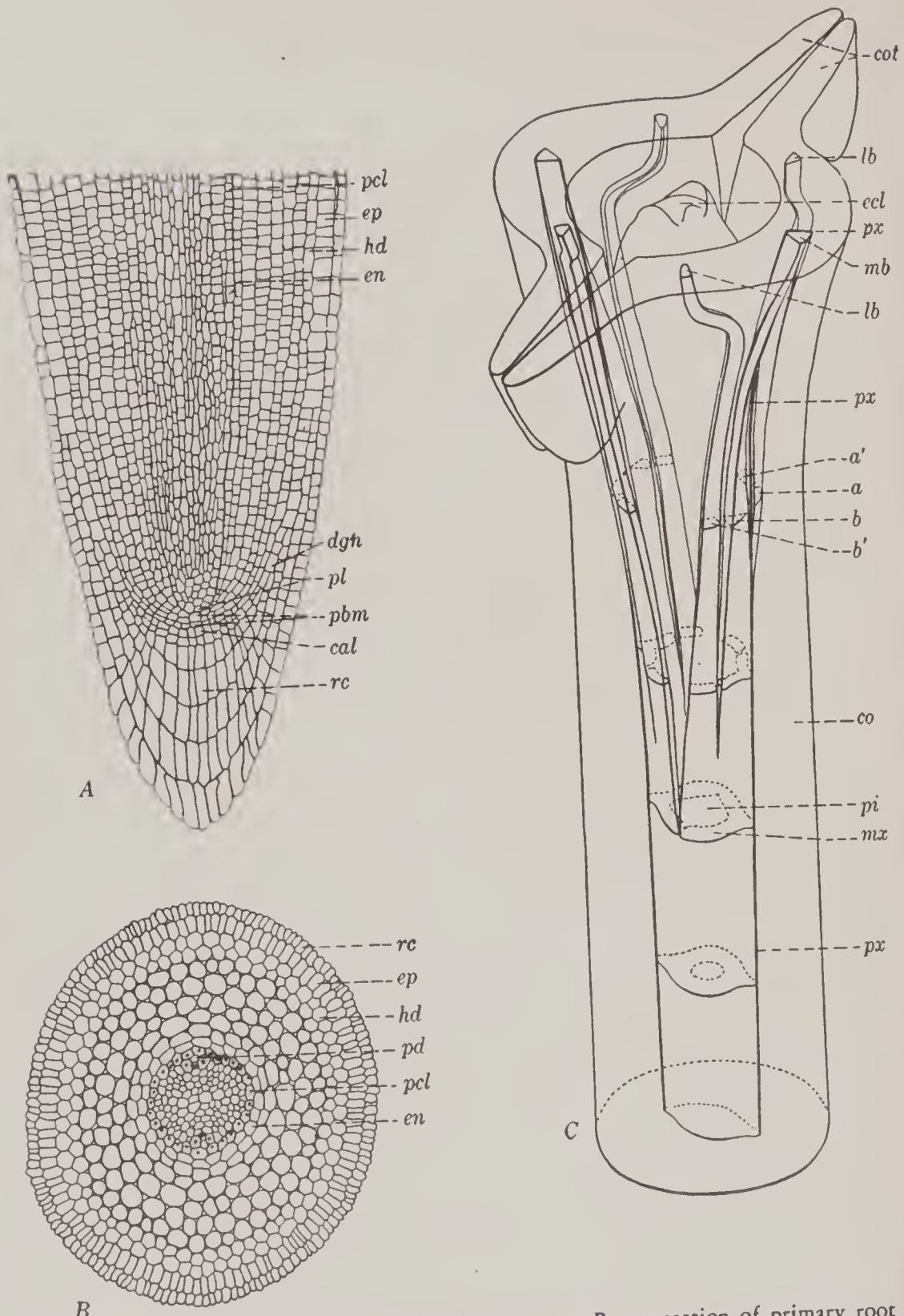


FIG. 194. *A*, median longisection of primary root; *B*, transection of primary root 0.7 mm. from tip; *C*, schematic diagram of hypocotyl showing vascular transition from root to cotyledons; *a*, *b*, bundles which anastomose and form double bundle of cotyledon; *a'*, *b'*, lateral metaxylem elements which form lateral bundles of cotyledons: *cal*, calyptrogen; *co*, cortex; *cot*, cotyledons; *dgn*, dermatogen; *ecl*, epicotyl; *en*, endodermis; *ep*, epidermis; *hd*, hypodermis; *lb*, lateral bundle to cotyledon; *mb*, median double bundle of cotyledon; *mx*, metaxylem; *pbm*, periblem; *pcl*, pericycle; *pd*, primary phloem duct; *pi*, pith; *pl*, plerome; *px*, protoxylem; *rc*, root cap. (After Crooks.)

opment and regeneration in the flax seedling, Crooks (7) has confirmed and elaborated Janczewski's work, and his detailed account of the root ontogeny is quoted.

"The calyptrogen-dermatogen layer of cells overlying the periblem multiplies by periclinal divisions around the tip and forms a root cap of regular, radial rows of cells. In the lateral portion of the same layer the epidermis is formed by anticlinal divisions. Laterally, where the divisions are anticlinal the histogen is strictly a dermatogen, while the layer at the tip is a calyptrogen. The root cap at the tip is very regular because the cell divisions in the calyptrogen are periclinal only. Occasionally, some of the cells in the lateral portion of the root cap divide anticlinally and distort the radial rows. This occurs only in lateral portions of the root cap and not at the tip, where the rows of cells are regular.

"The cortex is derived from the periblem, which consists of two layers of cells overlying the plerome. The outermost layer of the periblem divides only anticlinally and forms the outer layer of the cortex, the hypodermis. The inner layer divides in all planes and forms the remainder of the cortex, which at maturity is about 6-9 cells in thickness. (Fig. 194, A.)

"The stele is differentiated from a small group of plerome cells which divide in all planes at the tip, while divisions at a higher level are chiefly in a transverse plane. The outer layer of this group produces the pericycle, which can be distinguished rather early by the relatively dense cytoplasm and larger size of the cells. The first evidence of differentiation of the vascular system appears about 0.4 mm. above the tip of the plerome. Two primary phloem ducts are first differentiated opposite each other by the elongation and breakdown of a single row of cells lying next to the pericycle, and alternate with the two protoxylem points which are differentiated later. Figure 195 shows how these ducts are formed and stretched by the elongation of neighboring cells. These ducts collapse after becoming greatly stretched but usually persist until the protoxylem elements are well differentiated. Elongation of the root often causes the protoxylem to collapse. The

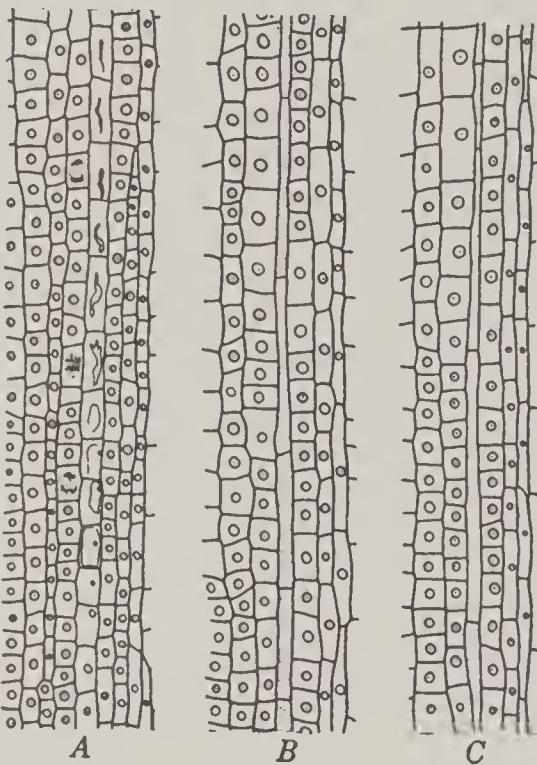


FIG. 195. A, B, and C, longisections of portions of primary root showing formation of primary phloem duct at 0.61, 1.0, and 1.5 mm. from tip respectively. (After Crooks.)

metaxylem elements differentiate centripetally until all the elements of the xylem plate are lignified and no central parenchyma remains. The outermost metaxylem elements have scalariform wall thickenings while those centrally located have pitted wall thickenings."

THE ORIGIN OF LATERAL ROOTS. — The lateral roots are initiated at about the time that the secondary wall thickenings of the metaxylem elements are being laid down. The first secondary root primordia occur just below the soil level and are oriented in the plane of the protoxylem strands or more frequently slightly to one side of them. The cells of the pericycle adjacent to the protoxylem points undergo tangential divisions which result in the production of two distinct layers. (Fig. 196, *A*, *a* and *b*.) The cells of each of these layers divide tangentially so that the root primordium is four layers in width as seen in a transection of the primary root. (Fig. 196, *B*.) The divisions of the first two layers do not take place simultaneously, and ordinarily the inner layer divides somewhat in advance of the outer one. In order to compensate for the increasing length of the overlapping layers, a few radial divisions occur in the root primordium but these take place in such a way that they cause no distortion of the tangential alignment of the rows of cells. The four layers, derived from the pericycle, function as histogens: the outer one *a'* becomes the calyptrogen-dermatogen layer; the next one *a''* functions as the periblem; and the two inner ones *b'* and *b''* give rise to the plerome.

While the growing point of the lateral root is differentiated from pericyclic derivatives, the adjacent cells of the endodermis divide radially to compensate for its enlargement. This anticlinal division of the endodermal cells continues so that it persists as a single layer of cells about the tip of the lateral root. (Fig. 196, *E-H*.) It never becomes more than one cell layer in thickness, but maintains its position until the lateral root penetrates through the cortex of the primary root and into the soil, when it disintegrates, together with the outermost layer of the root cap. As the lateral root penetrates the cortex, there is little accumulation of debris or distortion of the cortical cells, which indicates that the emergence of the lateral root involves some digestion as well as mechanical crushing of the cortical tissues.

In tracing the subsequent development of the histogens, Crooks has pointed out that the two inner layers constituting the plerome continue to divide in all planes and produce a conical group of cells

which differentiate stelar tissue in the same manner as occurs in the primary root. (Fig. 196, D.) The stele is diarch and the primary

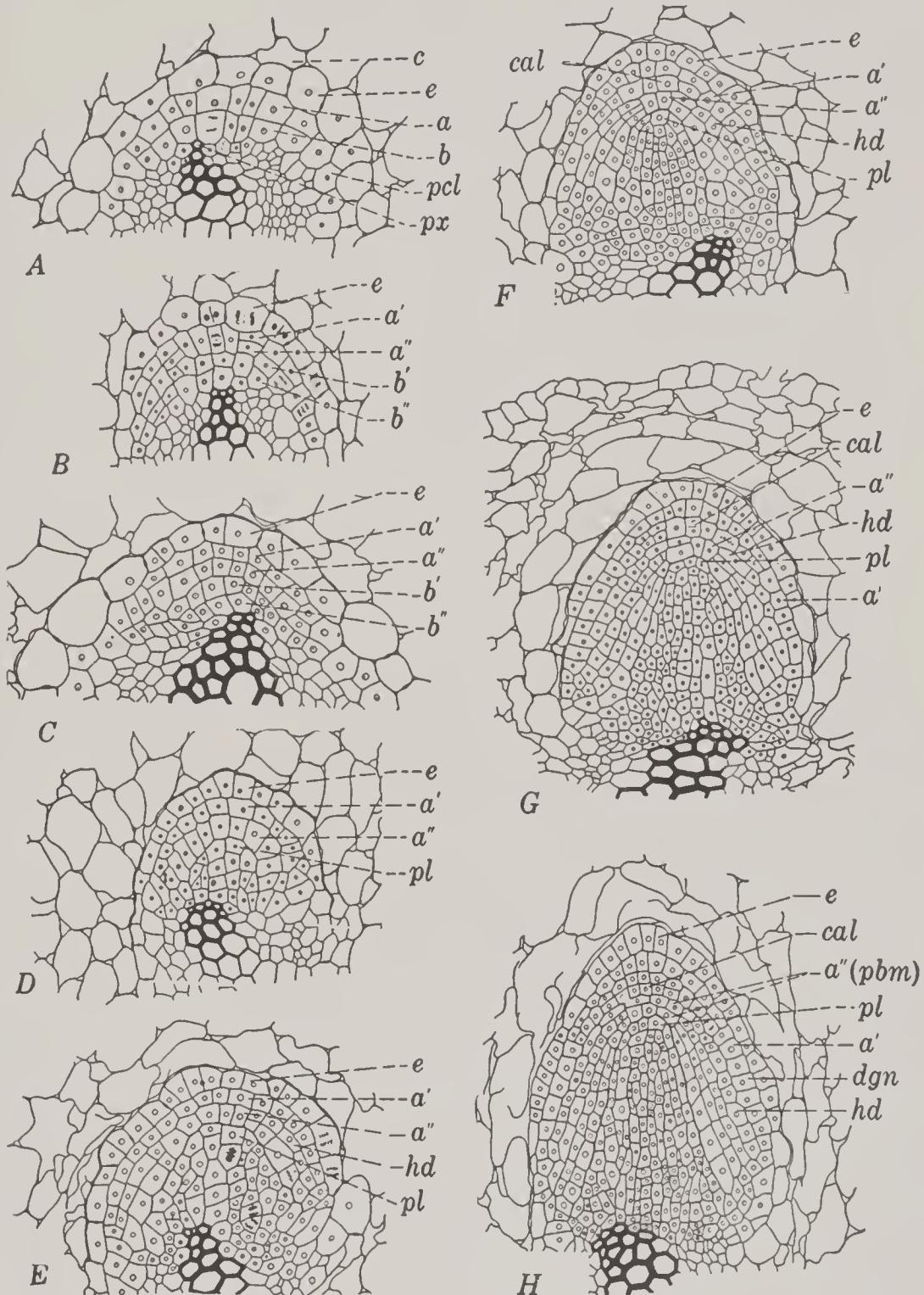


FIG. 196. *A-H*, transections of young primary roots showing origin of lateral roots; *a*, outer layer of first two layers derived from pericycle; *a'*, outer layer derived from *a*; *a''*, inner layer derived from *a*; *a''(pbm)*, periblem; *b*, inner layer of first two layers derived from pericycle; *b'*, outer layer derived from *b*; *b''*, inner layer derived from *b*; *c*, cortex; *cal*, calyptron; *dgn*, dermatogen; *e*, endodermis; *hd*, hypodermis; *pcl*, pericycle; *pl*, plerome; *px*, protoxylem. Derivatives of layer *a'* become calyptron and dermatogen; those from layer *a''* become periblem; and those from layer *b*, plerome. (After Crooks.)

xylem strand of the lateral root lies in the same plane as the strand of the root axis from which it originates.

As the plerome increases in size, anticlinal divisions occur in the two outer layers of the pericycle (a' , a'') to compensate for this growth, and the innermost of these two layers (a'') begins periclinal divisions at a point farthest removed from the tip. These periclinal divisions occur progressively in this layer toward the tip of the primordium; and, subsequently, their innermost derivatives also undergo periclinal divisions. This stage is illustrated at the right in Figure 196, *E*, where the basal portion of the layer a'' has divided once and one of the innermost derivatives is undergoing another division as indicated by the mitotic figures. In this manner, the number of cell layers is increased by successive periclinal divisions from the newly formed layers of the periblem. (Fig. 196, *F.*) In each instance, the divisions of the inner layers are continued progressively toward the tip of the root; and, finally, the remaining cells of layer a'' are all divided once periclinally and the basic plan of the periblem is established which is similar to that described for the primary root. (Fig. 196, *H.*) The outermost layer of the periblem divides only anticlinally, producing a single layer which differentiates into the hypodermis. At the tip of the root, the innermost layer of the periblem continues to divide and produces the other six to eight layers of cortical cells, the innermost becoming the endodermis.

By the time that the periblem has formed about three cell layers around the base of the conical plerome, the outermost one, a' , undergoes periclinal divisions at its tip. (Fig. 196, *F.*) Of the two layers thus formed, the outer one becomes the first layer of the root cap, while the inner one remains meristematic and by further divisions produces additional layers of the root cap. As in the primary root, the laterally oriented cells of the layer a' continue anticlinal divisions and function as a dermatogen which gives rise to the epidermis. Following the establishment of the histogens, subsequent stages in the ontogeny of the lateral root are similar to those of the primary root.

VASCULAR TRANSITION. — Vascular transition takes place in the hypocotyl although the stelar tissue is not completely collateral and endarch until the bases of the cotyledons are reached. At approximately the ground level, the stele of the lower hypocotyl is root-like with a diarch primary xylem strand, laterally placed

phloem groups, and no central pith; but above this point, the center of the axis is parenchymatous and there is a gradual reorientation of the vascular elements. (Fig. 197, A.) Each of the phloem groups divides to form four phloem regions in the lower one-fourth of the hypocotyl; and, at a higher level, they become

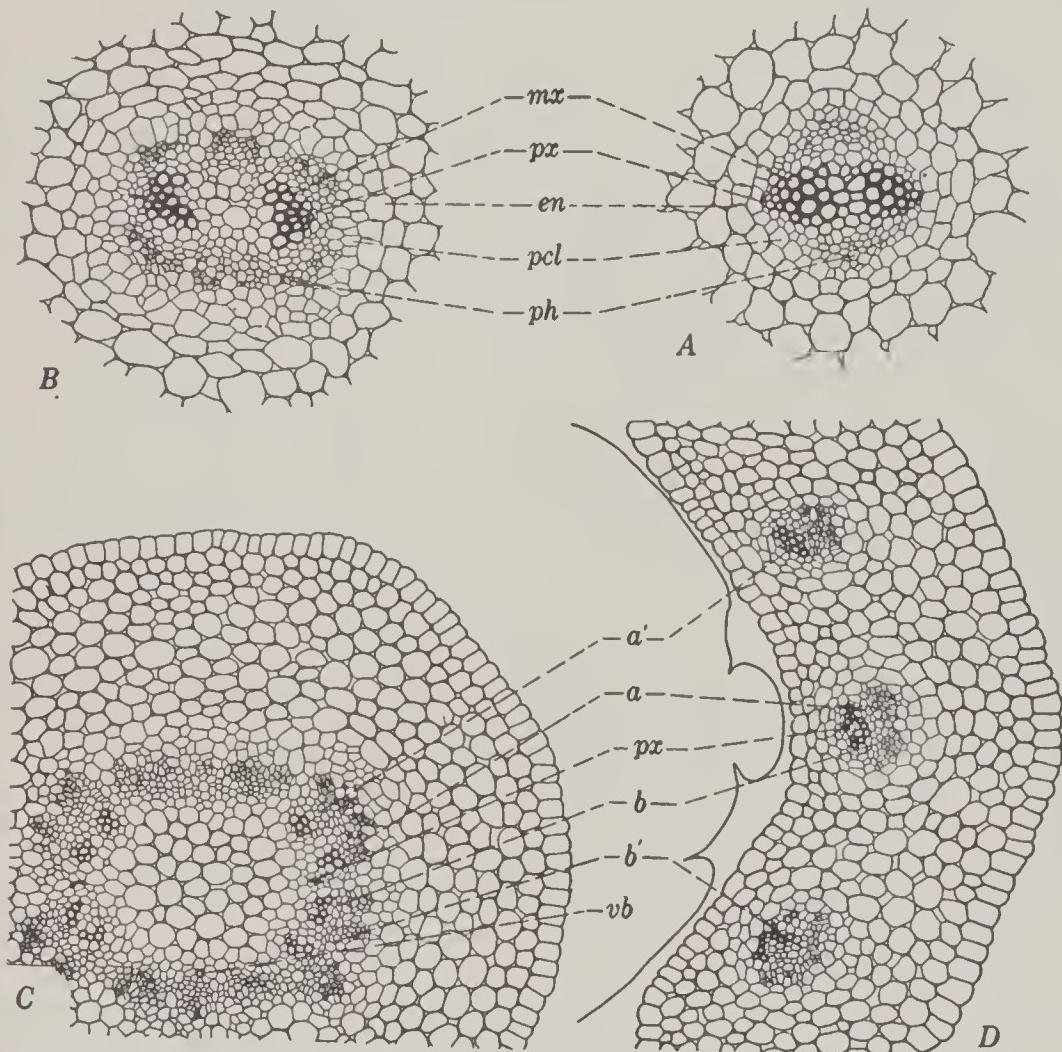


FIG. 197. A-D, transections of six-day seedling showing vascular transition: A, about 2 mm. below ground level; B, middle hypocotyl showing parenchymatous pith and disintegration of protoxylem; C, upper region of hypocotyl showing eight metaxylem groups with associated phloem; D, at base of cotyledon and epicotyl showing vascular bundles of cotyledon: *a*, *b*, bundles which anastomose to form double bundle of cotyledon; *a'*, *b'*, lateral bundles of cotyledon: *en*, endodermis; *mx*, metaxylem; *pcl*, pericycle; *ph*, phloem; *px*, protoxylem; *vb*, vascular bundle of first foliage leaf. (After Crooks.)

equally spaced at about 90° intervals from one another. (Fig. 197, B.) The primary phloem of the leaf traces of the first two foliage leaves is downwardly differentiated into the hypocotyl and anastomoses with the phloem of the cotyledonary bundles at about the point where the phloem groups of the lower hypocotyl are branched.

Coincident with the reorientation and branching of the primary phloem, the metaxylem elements are differentiated in a more and more tangential position in relation to their respective protoxylem points. There are four metaxylem groups, each of which is adjacent to a phloem strand and centrad to it. At about the mid-point in the hypocotyl, the four metaxylem groups and their collateral phloem strands are each bifurcated so that eight vascular bundles are formed which constitute the cotyledonary traces. At higher levels, two groups, each of four metaxylem strands, are formed; and these become oriented in a more nearly lateral position with respect to the protoxylem poles. As this reorientation of the two groups of cotyledonary bundles proceeds, they become widely separated, each group of four bundles constituting the vascular supply to a cotyledon. (Fig. 197, C.)

At the cotyledonary node, the two lateral bundles of metaxylem and the accompanying phloem in each group of four, become more widely separated from the two centrally located ones, and continue without branching or anastomosing into the cotyledons forming the lateral veins. At higher levels, the two centrally located metaxylem groups are oriented in a more centrad position with reference to the protoxylem; and, at the point of divergence of the cotyledons, the primary xylem is endarch. The two metaxylem groups anastomose, forming the median double bundle of each cotyledon; but the two phloem groups of each double bundle are distinct at this level, anastomosing 2 or 3 mm. farther up in the cotyledon. (Fig. 197, D.)

The vascular system of the epicotyl is differentiated somewhat later than that of the cotyledons and hypocotyl. The bundles which constitute the traces of the first foliage leaves above the cotyledonary plate are differentiated as endarch, collateral bundles and extend downward into the hypocotyl where they may anastomose with groups of metaxylem and phloem; but, in some instances, end blindly in the parenchymatous tissue.

There is disintegration and a partial or complete resorption of the primary xylem in the seedling axis, similar to that described for *Allium* by Chauveaud (5) and Hoffman (12); and because of this ephemeral character of the primary xylem, Crooks used plants about six days old. In older axes, the protoxylem is first crushed and stretched; later, in the upper and middle hypocotyl, the first-formed metaxylem disintegrates; and, ultimately, nearly all of the

primary xylem disappears. The stretching of the spiral elements results in their collapse; and, in plants two weeks old, practically all of them in the upper hypocotyl are obliterated. (Fig. 198.) However, fragments of the primary xylem may remain for longer periods, or throughout the life of the plant, without being com-

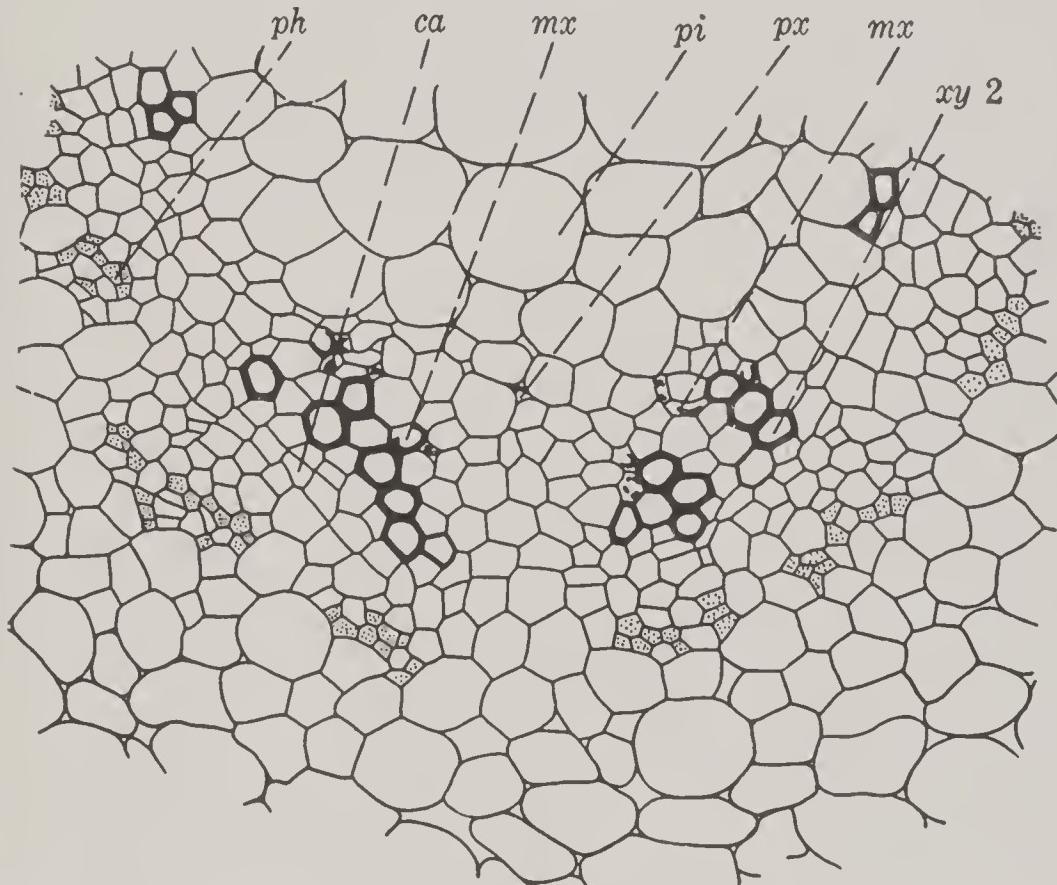


FIG. 198. Transection of portion of vascular ring in upper hypocotyl showing early dis-integration and resorption of primary xylem: *ca*, cambium; *mx*, metaxylem; *ph*, phloem; *pi*, pith; *px*, protoxylem; *xy 2*, secondary xylem. (After Crooks.)

pletely resorbed; and may be seen, especially in longisection, among the parenchymatous cells.

THE COTYLEDONS. — The obovate cotyledons are subsessile, and, in young seedlings, are somewhat broader than the hypocotylodonal axis at their point of divergence. The mesophyll is made up of very compact storage cells, two or three of the adaxial layers forming a palisade region while the lower four or five layers are more rounded and compact. There is an early differentiation of the protoxylem elements in the median bundle; and under favorable conditions they are completely matured twenty-four hours after germination. Cases have been observed where some of the protoxylem is differentiated in the mature seed, and scattered phloem elements occur in the provascular strands of the immature cotyle-

dons before wall thickenings can be observed in the primary xylem.

After emergence above the ground, the cotyledons enlarge and thicken for about two weeks, persisting for a longer period than do many seedlings; but, in about thirty days, they become yellow and die. The mesophyll of the mature cotyledon resembles that of a foliage leaf, except that it is thicker and the intercellular spaces are smaller. Stomata occur in considerable numbers in both the upper and the lower epidermis and are subtended by large air spaces. The venation is closed, resembling that of the leaf; and, except at

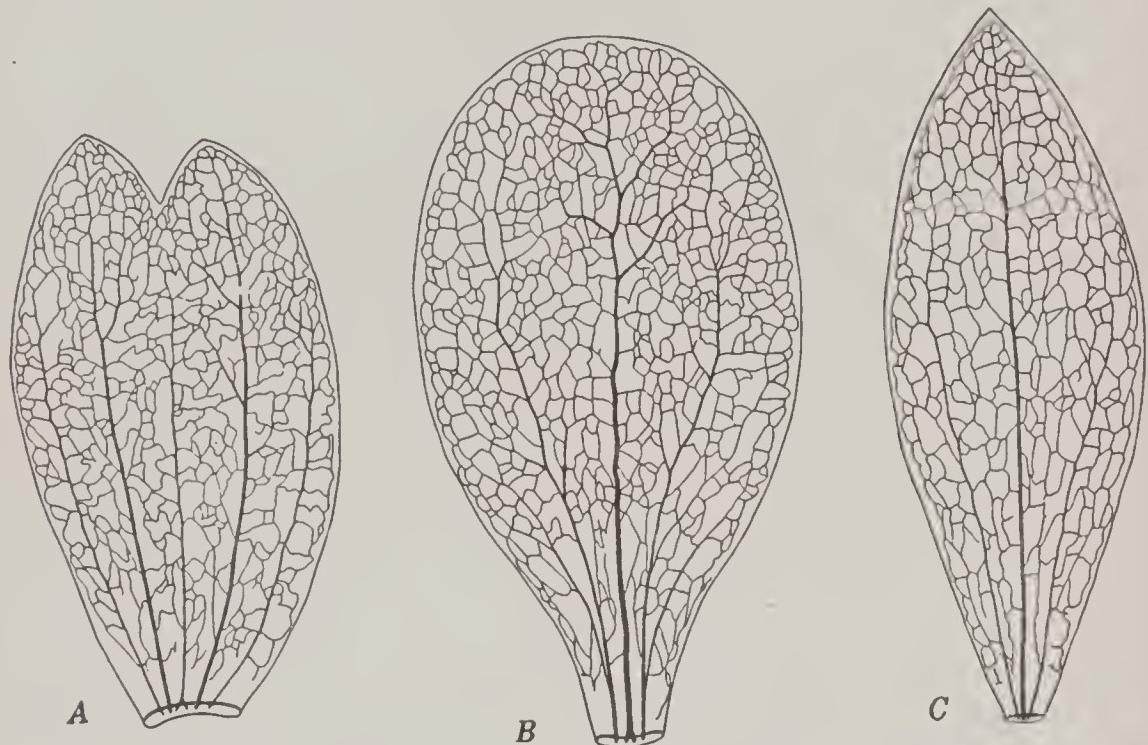


FIG. 199. A-C, diagrams showing venation: A, double leaf; B, cotyledon; C, typical foliage leaf. (After Crooks.)

the base of the median vein, all of the bundles are collateral. (Fig. 199, B.)

ONTOGENY OF THE LEAF. — The epicotyledonary axis develops very slowly for the first eight or ten days and is surrounded by the bases of the cotyledons. The leaf primordium involves at least three of the outermost cell layers at its point of origin, arising from the growing point as a conical mass of cells which elongates and broadens, due to general meristematic activity, and becomes a somewhat flattened subconical projection. (Fig. 26.) Continued general cell division increases the length of the flattened primordium, until it is about one-fifth the length of the mature leaf; and then a localization of meristematic activity to the lateral

and adaxial portions of the primordium results in the formation of the lamina. As this proceeds, the cells of the mesophyll undergo enlargement, and the procambial strands, which were determined early in ontogeny, differentiate as vascular bundles.

The meristematic activity does not cease at one time throughout the developing leaf, but is discontinued first at the tip of the leaf, then at its base, and finally in the midbasal portion of the lamina. (Fig. 200, A, B, C.) Following the cessation of cell division, which occurs when the leaf has attained about one-fifth its mature size, further enlargement is accomplished by the expansion, stretching, and separation of the cells already formed, and, at maturity, the mesophyll is very loose and spongy with large intercellular spaces. (Fig. 200, D.) It consists of about four cell layers which are not differentiated into a well-defined palisade and spongy parenchyma, and the cells are all somewhat elongated and essentially alike. A network of veins extends throughout the mesophyll, forming a complicated system made up of bundles of various sizes. The midvein and occasionally the two larger lateral veins may develop some secondary tissue. The epidermal cells are irregular in size with a thin cuticle, and numerous stomata occur in about equal numbers on both surfaces of the leaf. The guard cells are subtended by accessory cells in which, as pointed out by Haberlandt (9), the thin walls act as hinges in the stomatal mechanism.

The successive leaf primordia are at first very close to one another so that there may be ten to twenty nodes and internodes in a growing point which is only 0.1 to 0.15 mm. in length. The provascular tissue of the epicotyl appears to be differentiated simultaneously in the leaf primordia and meristematic tissue of the growing point, and each strand extends downward through the axis for several internodes, keeping pace with internodal elongation so that there is no change in the fundamental plan of the vascular system as differentiation proceeds.

All the bundles of the mature vascular system are collateral and common. The vascular supply to each leaf consists of three large bundles which pass through the cortex separately, anastomosing with one another at the point where they form a part of the stele of the stem, and gradually becoming smaller at lower levels until they end blindly after extending through fifteen to twenty nodes. There are usually eight to ten foliar bundles which extend through

the cotyledonary node and into the hypocotyl; and, of these, the bundles from the first pair of leaves above the cotyledons may

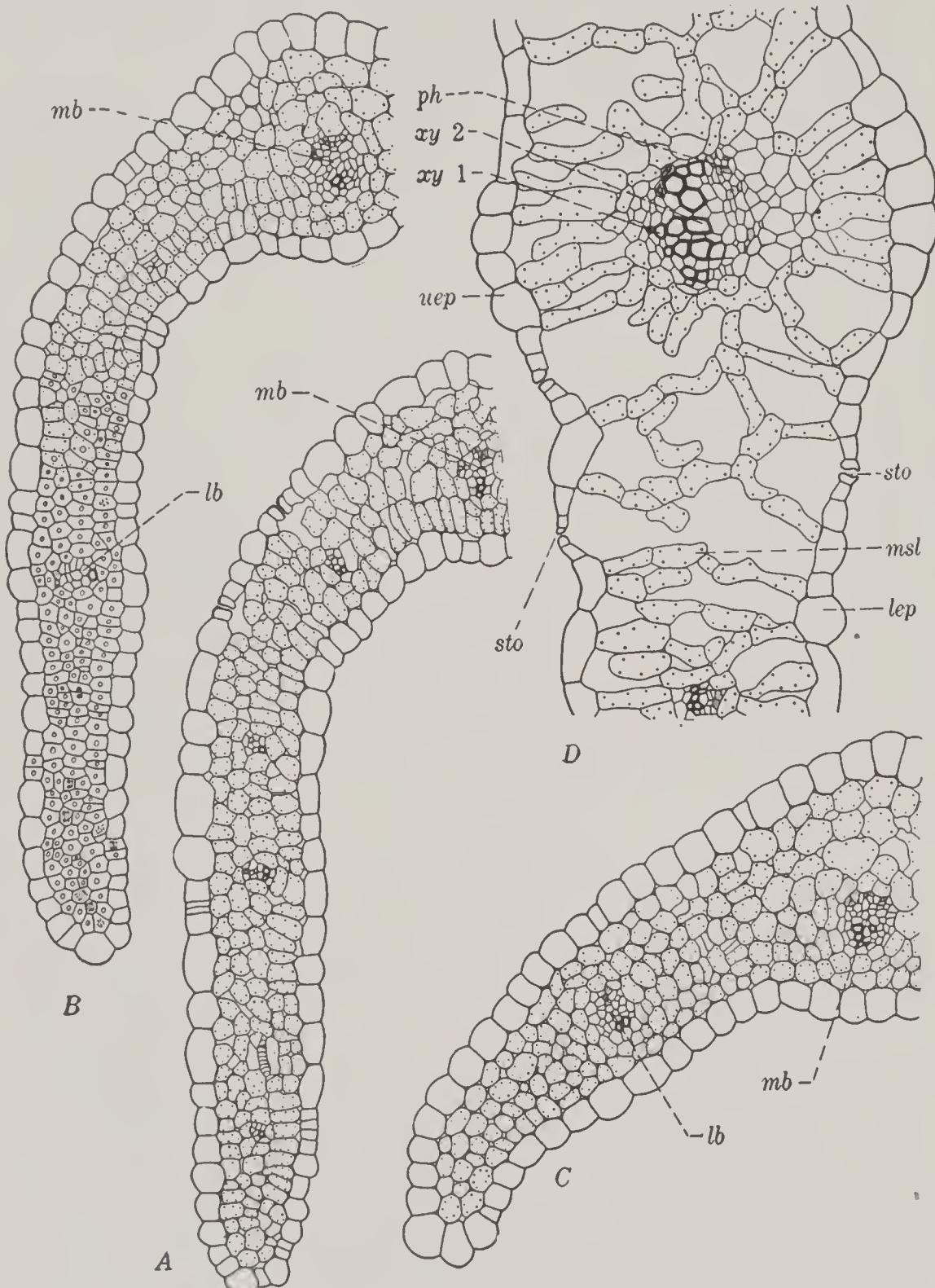


FIG. 200. A, transection of first leaf 0.9 mm. from tip where cell divisions have ceased; B, transection of same leaf 0.18 mm. from tip showing meristematic activity in lamina; C, transection 0.1 mm. from base of same leaf showing level where cell divisions have ceased; D, transection through median vein of mature leaf from middle region of stem: *lb*, lateral bundle; *lep*, lower epidermis; *mb*, median bundle; *msl*, mesophyll; *ph*, phloem; *sto*, stoma; *uep*, upper epidermis; *xy 1*, primary xylem; *xy 2*, secondary xylem. (After Crooks.)

anastomose with the lateral arches of metaxylem in the root-like portion of the lower hypocotyl while the others end blindly. Interconnections between the bundles of the stem are accomplished, following the maturation of the primary tissues, by the development of fascicular and interfascicular cambiums which produce a continuous cylinder of secondary vascular tissue.

THE STEM. — In the United States, relatively little investigation of the structure of the stem and its fibers has been carried on; but in Europe, where fiber production is more important, extensive studies have been made. The most desirable stems for fiber purposes are those which, in addition to having the genetic qualities necessary for good fiber production, have been grown closely together so that the stems are long, slender, and unbranched. In such cases, the diameter of the mature stem of fiber flax may not exceed 2 or 3 mm.; but it may be considerably greater under unfavorable cultural conditions, or in the more branched, stocky types of flax that are grown for seed.

The young stem is round or subterete in transection; and, as it matures, it becomes hollow due to a progressive disintegration of the centrally located parenchymatous cells. The relatively large, thick-walled epidermal cells have a well-defined cuticle; their tangential dimension is about twice the radial one; and they are elongated in the axial direction, being several times as long as wide. The stomata which occur in longitudinal rows are somewhat depressed, and the guard cells are subtended by crescentic accessory cells that form a part of the motor mechanism as in the leaf. Tammes (21) reports a stomatal frequency of 30–40 per sq. mm., while Herzog (11) records counts of 25–35.

Within the epidermis is a single-layered hypodermis in which the cells resemble those of the former, but are much smaller and thinner walled. The hypodermal cells contain chlorophyll, and are compact rather than having the spongy organization of the other four or five layers of chlorenchyma lying between the hypodermis and the endodermis. The spongy cells are approximately isodiametric and arranged in longitudinal rows that may be more or less separated depending upon the age of the stem. As the stem becomes older, the epidermis persists, its component cells undergoing radial divisions without rupturing, while the cortical cells first become tangentially elongated and then much crushed and radially compressed. The large, oval endodermal cells can be

readily distinguished in the young stem by their dense cytoplasmic contents.

The pericycle at first consists of a single layer of thin-walled cells, but later forms a multiseriate zone between the endodermis

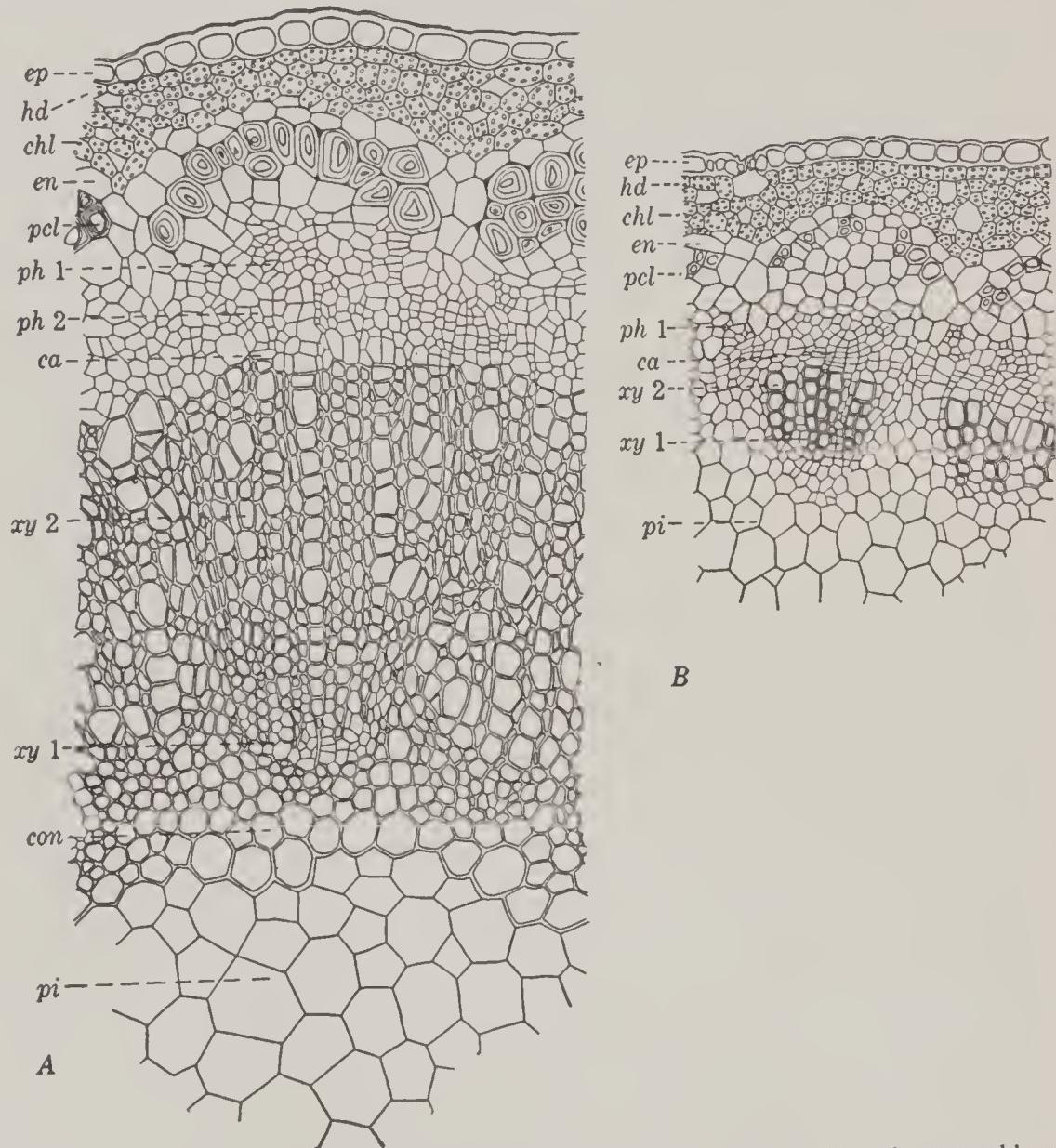


FIG. 201. *A*, transection of sector of mature flax stem; *B*, transection of comparable sector of young stem: *ca*, cambium; *chl*, chlorenchyma; *con*, connective tissue; *en*, endodermis; *ep*, epidermis; *hd*, hypodermis; *pcl*, pericyclic fibers; *ph 1*, primary phloem; *ph 2*, secondary phloem; *pi*, pith; *xy 1*, primary xylem; *xy 2*, secondary xylem.

and the phloem, and in this region groups of fibers develop which constitute the fiber bundles of commerce. The development of the pericyclic fibers is centripetal, the first ones differentiated being adjacent to the endodermis, while the later formed ones abut the phloem. (Fig. 201.)

The vascular bundles form a dissected siphonostele in which

adjacent bundles are separated from one another by medullary rays one to several cells in width. As the stem matures, the activity of the fascicular cambium, together with the initiation of an interfascicular cambium, results in the formation of a continuous cylinder of secondary xylem. In addition to this, there is a thickening of the walls of the ray parenchyma, as well as of the medullary parenchyma surrounding the primary xylem points, so that connective tissue also contributes to the continuity of the mechanical elements of the stele. The remaining cells of the medulla, aside from the centrally located ones which disintegrate, are large and thin-walled.

The number of primary xylem elements in a single bundle is not large, the protoxylem consisting of a few annular, annular-spiral, and spiral types. As the stem matures, the rings in the annular elements are usually distorted or partially obliterated, and the spirals in the other types become much stretched as the internodes elongate. The metaxylem elements are scalariform and reticulate, while the secondary xylem vessels are pitted with vessel segments that commonly have oblique end walls. The cells of the xylem parenchyma are much elongated axially and have transverse end walls. The phloem consists of slender sieve tubes, companion cells, parenchyma; and occasionally phloem fibers, but the latter have no commercial importance. (Fig. 202.)

THE ONTOGENY OF THE FIBER — INITIAL STAGES. — The fibers are differentiated in the pericyclic region, and the initial stages in their ontogeny take place just below the meristematic growing point of the stem axis. In longisection, the pericyclic cells can be distinguished from the endodermal cells which lie immediately outside them, since the former do not divide transversely as frequently as the latter, the pericyclic cells compensating for the increase in the length of the axis by cellular elongation rather than by division. Early in ontogeny, however, the initial pericyclic cells do divide periclinally several times so that this zone becomes a multilayered region of large, thin-walled, elongated cells.

Anderson (2) has pointed out that the

"enlargement phase of fiber development involves two types of increase: an early, rapid, and extensive increase in diameter and length; and a slow but perceptible increase in diameter, limited to certain cells, that continues during the life of the plant."

While some investigators have expressed doubt regarding the second type of growth, critical experiments by Tammes (21) indicate that as the stem increases in length, there is also an increase in fiber diameter. This increase does not occur at a uniform rate, being much more rapid in the initial stages of fiber development than during the later phases of maturation. She found that as the stem increased from 1 mm. up to a height of 77 cm., the average diameter of the fiber increased from 11.6μ to 32.0μ . Anderson (2)

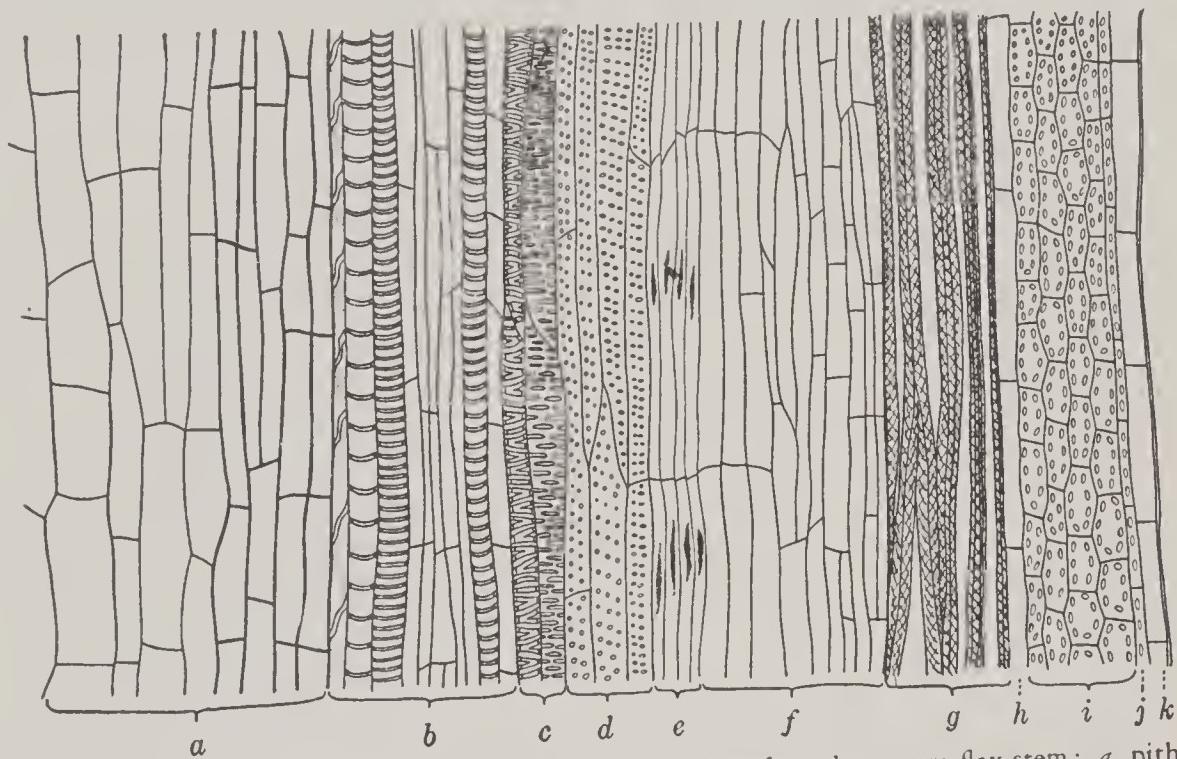


FIG. 202. Semi-diagrammatic longisection of portion of nearly mature flax stem: *a*, pith cells including thick-walled connective cells adjacent to xylem; *b*, protoxylem elements and xylem parenchyma; *c*, metaxylem; *d*, secondary xylem; *e*, cambium; *f*, phloem zone including secondary and primary phloem; *g*, pericyclic fibers; *h*, endodermis; *i*, chlorenchyma; *j*, hypodermis; *k*, epidermis.

compared measurements of young and mature fibers and concluded that developmental increases in fiber size were not common for all fiber cells, occurring more conspicuously in some than in others. He states that there is no doubt but that fibers do undergo "a slow increase in diameter during their development until the time that deposition of cell-wall material ceases."

The length and diameter which the fiber attains are variable, depending upon variety and cultural conditions. Diameters range from 12 to 25μ . Matthews (15) and Cross and Bevan (8) have reported average lengths of 25 to 30 mm., Haberlandt (9) 20 to 40 mm., Wiesner (27) 20 to 50 mm., Herzog (10) 1.7 to 53.9 mm.,

and Tammes (21), extremes of 1 to 120 mm. with averages approximating those of other investigators. The extreme lengths of the individual fiber cells are based upon their continued independent growth. Tammes (21) points out that the pericyclic cells which differentiate into fibers do not undergo any transverse division, or at least not as frequently as adjacent cells, and continue to elongate without cross wall formation. This general growth proceeds until the basal portion of the cell is below the region of axial elongation of the meristematic portion of the stem tip, and then that part of the fiber ceases to elongate, further increase in length being restricted to the upper portion of the fiber. Theoretically, the pericyclic cell may continue to elongate as long as the adjacent cells are dividing transversely and the axis in that locus is undergoing internodal elongation; but, actually, there are occasional transverse divisions. In connection with secondary wall thickening, there may be a peculiar separation of portions of the protoplast by secondary layers of cellulose which results in local dilations in the fibers. (Fig. 203, D, 1-4.)

In addition to the method of fiber elongation described by Tammes (21), Anderson (2) believes that there is a sliding action by which the tips of the elongating pericyclic cells push past one another. It seems likely that this phase of elongation accompanies general cellular enlargement. The tips of the fibers are not transverse, but taper gradually to a very acute point, and the length of the tapered portion of the fiber may indicate the approximate amount of sliding that has occurred. (Fig. 203, D, 5.)

GROWTH AND WALL FORMATION OF THE FIBER.—The wall structure of the flax fiber has been the subject of intermittent investigation since Nägeli (16) observed the concentric lamellae and alternating light and dark bands in its secondary walls. Subsequently, Krabbe (14), Correns (6), Tammes (21), Nodder (17), Aldaba (1), Anderson (2), and others have each added something to an understanding of fiber structure and development.

The middle lamella consists of pectic materials deposited by the split halves of the cell plate when wall formation is initiated. Herzog (11) and others interpret it as being *intercellular* substance, applying the term *primary wall* to the first deposits of material against the middle lamella and using the term *secondary wall* in referring to the lamellated structures deposited later. (Fig. 203, A-C.) There has been some confusion in cell wall terminology

(Chapter I), but it is clear that the first phase of growth involves a rapid elongation and enlargement of the fiber cell and a slight increase in the thickness of the cell wall resulting from additions of cellulose to the middle lamella. Adjacent to the middle lamella

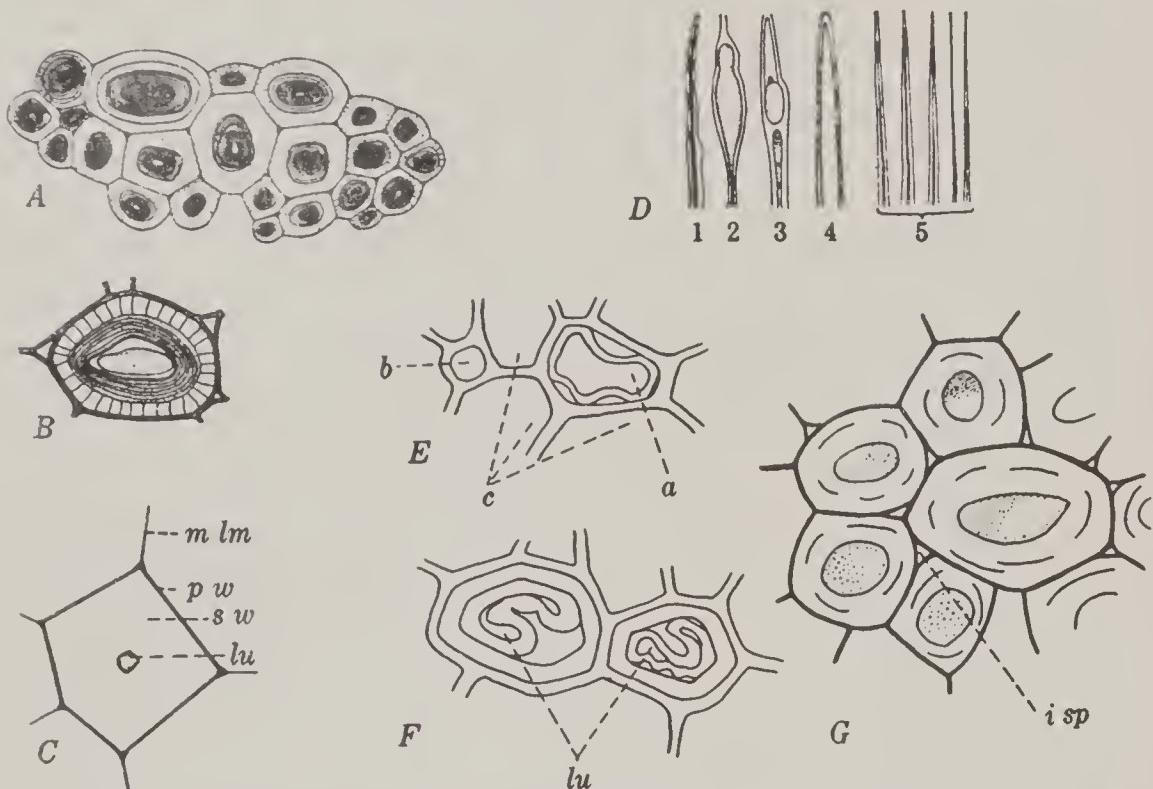


FIG. 203. Structure of fiber: *A*, transsection of group of fibers showing middle lamellae and concentric layers of secondary wall with delicate reticulated structure; *B*, transsection of single fiber showing primary wall and two layers of secondary wall, innermost of which is divided into seven lamellae; *C*, diagram of fiber in transection showing lumen, *lu*, middle lamella, *m lm*, primary wall, *p w*, and secondary wall, *s w*; *D*, longitudinal views of ends of fibers (fibers 1-4 illustrate abnormal forms from basal portion of stem, while those in group 5 are normal types); *E*, *F*, and *G*, transections of progressive stages in development of fiber; *E*, transections of young fibers showing, *a*, fiber with infolded inner wall layer; *b*, point of fiber in transection, and *c*, fiber cells still unthickened; *F*, transection of two mature fibers from lower part of stem showing infolded inner wall layers; *G*, transection of group of fibers from uppermost part of mature stem showing thickened primary wall, very thick secondary wall, and formation of some intercellular spaces, *i sp*. (*A*, *B*, *C*, *D*, redrawn from Herzog; *A* after Reimers; *B* after Krabbe; *Technologie des Textilfasern*, Julius Springer; *E*, *F*, and *G*, after Tammes, *Der Flaxsstengel*.)

there may be more or less pectic material which does not form a definite layer but is intermixed with the cellulose.

Cell wall formation is usually the result of an intussusception or apposition of wall substances, and it is by means of such processes that the primary and secondary walls of the fiber are probably laid down. However, it has been suggested by Aldaba (1) and Anderson (2) that these processes can hardly account for the formation of the successive lamellae which constitute the thickenings of the

flax fiber. Aldaba states that these may be formed by transformations of successive telescoping hyaline membranes which later differentiate into cell wall lamellae. According to this explanation, the lamellae are initially formed as a series of tubular membranes which overlie one another. Each successively formed membrane arises at the base of and centripetal to the previous one, growing upward toward the tip of the elongating fiber. These hyaline structures resemble plasma membranes, and are gradually transformed into lamellae which become thickened by a process suggestive of intussusception.

Anderson's explanation of the formation of the secondary layers agrees in many respects with that of Aldaba (1). He notes, that the first evidences of deposition of the lamellae occur at the basal portion of the fiber following the period of rapid elongation, that these layers are in contact with the remainder of the wall at only a few points or not at all, that the first cellulose deposited is much hydrated and in a state of viscosity that seems almost gelatinous, and that there is evidence to indicate that the wall formation actually occurs in the living cell free from adjacent walls of the same cell, later becoming coherent with them.

The process of secondary wall thickening is not a uniform one in which there is a steady increase in the thickness of the wall, but takes place as a series of periodic additions of new layers of cellulose. Each additional increment is deposited by the protoplast and appears in a transectional view of the fiber as a much involved and wrinkled layer which is apparently in contact with the previously formed secondary wall only at widely separated points or in some instances not at all. Later, it is pushed closely against this wall, but it does not adhere to it nor is there any welding material between them. The lamellae can be separated from one another, which indicates that they are not cemented together and emphasizes their independent origin. The force which causes the flattening out of the infolded layers is probably turgor pressure; and as a result of its action, the secondary wall loses its wrinkled appearance and becomes firm and more rigid. (Fig. 203, E-G.) Several lamellae are added in this manner, but they are not laid down with regularity and the number varies in different fibers.

The secondary wall is usually divided into two to five major layers, and these in turn may consist of many minute lamellae. The lines marking the limits of the major layers, as well as those

between the minute lamellae, have been described by Anderson as being the result of the periodicity of the deposition of wall materials.

"A series of lamellae is deposited by the protoplast, and then an interval of time intervenes before the next series of fine lamellae is laid down. This interval of time makes possible in the different layer divisions some changes in physical condition, and these differences are evidenced by slight variations in shades of color between them."

The layers of the secondary wall system are composed of unmodified cellulose which may vary in its physical condition depending upon its relative stage of development.

At maturity, the fiber cell consists of its constituent part of the middle lamella, the primary wall, and an extensive secondary wall. The middle lamella is originally composed of pectic substances, but undergoes changes as the fiber develops, the chief one being a tendency to become more or less lignified. The primary wall is largely cellulose, modified to some extent by pectose; and the secondary wall is made up of several (usually two to five) major layers of pure cellulose, which are in turn composed of thin layers that have been deposited in a manner that gives a definite striated appearance to the cell wall.

FIBER STRUCTURE. — Various details with respect to the characteristics of the fiber have been reported, including banding, which is a transverse marking or thickening of the fiber wall. This may be attributed to a wrinkling or folding of the cell wall; or, more frequently, the bands are the remains of primary thickenings which adhere to the secondary wall after retting. In addition to these fragments, there also may be particles of the walls of adjacent parenchymatous cells adhering to the fiber wall. Local displacements and distortions of the fibers also occur which appear to result from stresses involved in the manipulation of the fibers in retting or cutting rather than to any developmental factors. The minute spiral striations which can be observed on the surface of the fiber are related to the manner of wall formation, since the lamellae are made up of fibrils that are spirally arranged in the wall. The individual fibrils are below the resolving power of the microscope and the visible striations consist of groups of fibrils rather than of individual ones. Another feature of the physical structure of the secondary cell wall is that the direction of the spiral

striations in successive lamellae is alternately right- and left-handed.

FIBER LIGNIFICATION. — Lignification is not necessarily uniform in all the fibers in a given pericyclic area nor even in an individual fiber, and one fiber of a group may be strongly lignified while adjacent ones show little or no deposition of lignin. In general, the peripheral fibers in a group tend to be more strongly lignified than others; and it has been noted that this is also true of fibers located immediately centrad to a lenticel. In regard to the relation of lignification to the position of the fiber in the stem, it has been demonstrated that it is most extensive in the fibers at the base of the stem, and increases as the stem matures. This fact is of great importance in fiber flax because of its bearing on the process of retting and the final texture of the fibers. In instances where the flax becomes too mature, retting, which involves the decomposition of the middle lamella and the primary wall, is less complete and the fiber is coarse and harsh in texture.

Lignification is usually restricted to the middle lamella and primary wall; and there is little, if any, lignin in the secondary wall. This explains the fact that investigations, carried on to determine the degree of lignification, show the presence of more lignin in unretted fibers than in those which have been isolated by retting. The middle lamella is the first region to become lignified as the fiber matures, and lignification may stop at this point. In some cases, however, it involves portions of the primary wall, and may finally extend more or less completely through it. This decreases the commercial value of the fiber, as it is less easily prepared for market, and the fiber is of inferior quality, tending to be harsh and brittle instead of exhibiting the desirable qualities of smoothness, strength, and flexibility.

The chemistry of lignification is not entirely clear; but it has been suggested by Anderson (2) that it "is not a conversion of the cellulose directly into a lignified wall, but that the cellulose first undergoes a transformation to pectin-like substances."

VEGETATIVE REGENERATION OF THE PLANT. — As early as 1857, Reichardt (18) observed certain phases of vegetative regeneration in the shoots of flax, and these have been verified more recently by Tammes (21) in Holland. Beals (4), in describing the phenomenon of regeneration in flax, states, "first the epidermis divides and then the innermost row of those cells and the stimulated cells of

the region just beneath form the regenerated part, root or shoot." Crooks (7), in a detailed study, found specific differences in the ontogeny of adventitious roots and adventitious shoots.

ADVENTITIOUS BUDS. — When the growing points of young plants are injured or removed, the axis readily produces shoots; and when the injury occurs above the cotyledonary node, an axillary bud becomes active and produces a shoot. In his experimental work, Crooks removed all the organized buds by severing seedlings of various ages at different levels below the cotyledonary node, and in all plants which were not more than ten days old, from twenty to fifty adventitious buds developed on the remaining lower portion of each hypocotyl. This occurred even when the top of the plant had been removed to within a few millimeters of the ground level. In cases where plants two months old were similarly treated, approximately 60 per cent died without forming buds.

In seedlings less than ten days old, the origin of adventitious buds continues for six to eight days after the severing of the axis; and, since they are not all initiated at the same time, the hypocotyl may at one time have some adventitious buds which are large enough to show small leaves while others are in earlier stages of development. By the time that eight to ten of the buds have differentiated leaves, one of them usually outgrows the others. There is no spatial relationship of the dominant bud to any of the others, or to any special point on the hypocotyl, nor is the more rapidly growing bud necessarily the first one to be formed. Occasionally, more than one bud may continue development. The shoot which is formed by the growth of the adventitious bud develops an unbranched axis until the formation of the inflorescence; and it matures at about the same time as do plants of the same age which are uncut, but it attains only about one-half their height.

In the ontogeny of the adventitious bud, the first evidence of differentiation, following the abscission of the upper portion of the hypocotyl, is the formation of large intercellular spaces, resembling those of the mesophyll, in the cortical parenchyma of the hypocotyl. This occurs at the point of bud origin, and the bud is then initiated by the division of a single epidermal cell, quickly followed by a second division so that a four-celled primordium is formed. (Fig. 204, A, B.) Five or six of the epidermal cells adjoining the derivatives of the first meristematic epidermal cell

may also divide; and, after one or two more epidermal cells have become active, the underlying cortical cells lose their chlorophyll, become less vacuolate, and undergo cell division. (Fig. 204, *B*, *C*.) These cells continue division and growth so that the large intercellular spaces become occluded. Adjacent cortical cells

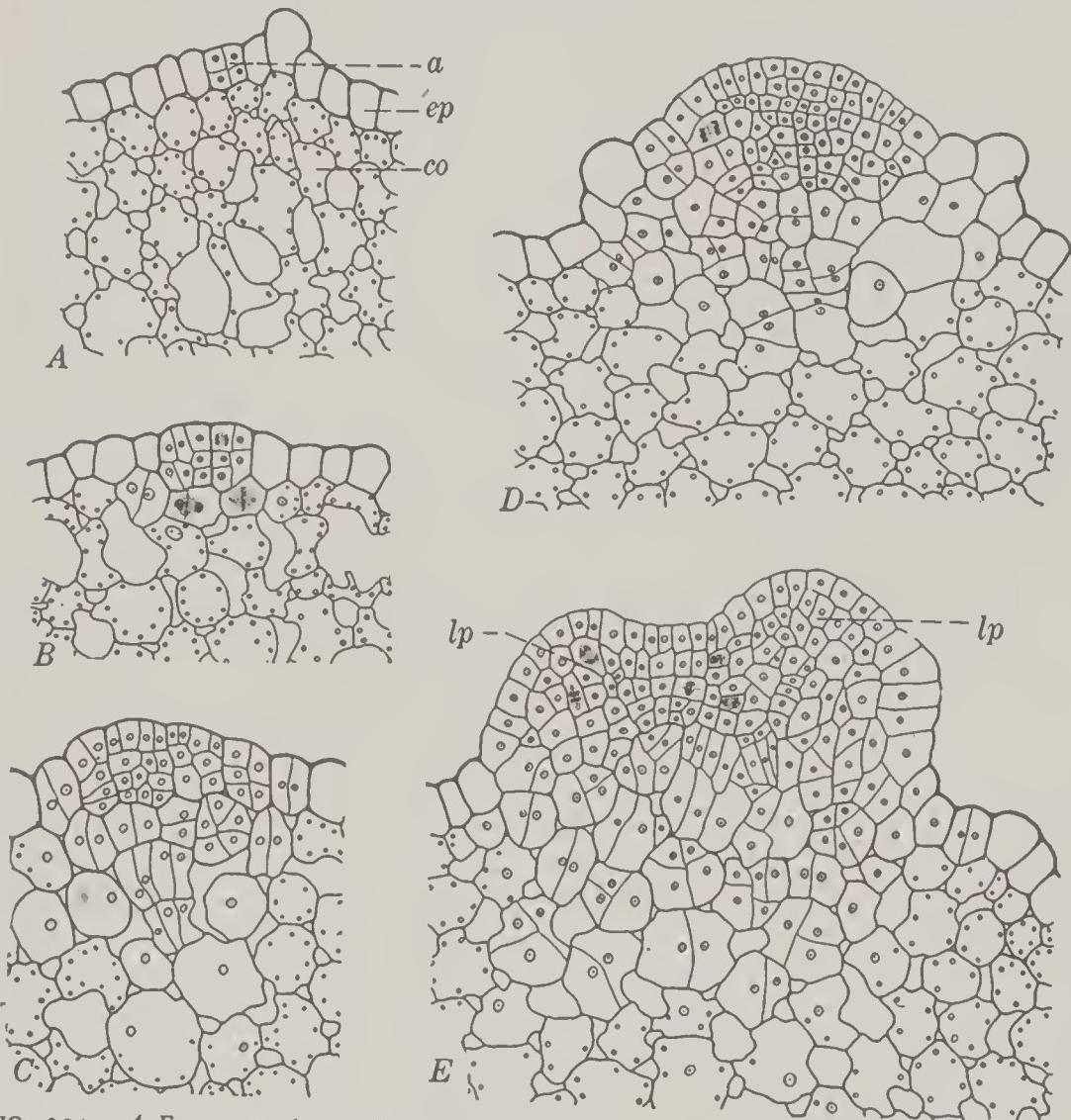


FIG. 204. *A-E*, transections of hypocotyl showing origin and development of adventitious buds after plant has been severed below cotyledons: *a*, four derivatives of a single epidermal cell; *co*, cortex; *ep*, epidermis of hypocotyl; *lp*, leaf primordia of adventitious buds. (After Crooks.)

are also activated, and this continues progressively in a centripetal direction until it has reached the endodermis. In this manner, a meristematic zone of compact cells is formed, extending from the epidermal bud primordium to the endodermis. Continued divisions of the cells of the primordium, derived from the original epidermal cells, produce a dome-shaped growing point, and this is followed by the rapid formation of two or three leaf primordia. (Fig. 204, *D*, *E*; and Fig. 205.)

The development of the first leaves of the adventitious bud is accompanied by a differentiation of their vascular elements so that protoxylem is present in them before cell division has begun in the inner layers of the cortex of the hypocotyl. (Fig. 206.) Following the proliferation of the parenchymatous cells of the inner portion of the cortex, the vascular tissue of the new bud is differentiated centripetally to the endodermis from some of the derivative cells thus formed. After several tracheids have been differentiated



FIG. 205. Longisection of hypocotyl showing development of adventitious bud after plant has been severed below cotyledons. (After Crooks.)

in this manner in the cortical parenchyma, a number of tangential and radial divisions occur in the endodermis. (Fig. 206.) Some of these endodermal derivatives differentiate as tracheids and establish continuity between the vascular system of the bud and tracheids which have differentiated from pericyclic cells and phloem parenchyma. The phloem associated with these newly differentiated tracheids consists chiefly of elongated parenchymatous cells, and by the time the vascular connection described above is completed, a layer of cells surrounding the tracheids begins to function as an active cambium. Within a few weeks, the secondary tissues

produced by this cambium, and the cambium of the hypocotyl proper, form a new plant axis which is almost straight.



FIG. 206. Longisection of hypocotyl showing development of adventitious bud after plant has been severed below cotyledons: *en*, endodermis. (After Crooks.)

ADVENTITIOUS ROOTS. — When seedlings six to ten days old are severed at the mid-hypocotyledonary region, and the upper part of the axis is set in moist soil with the cotyledons just above the soil level, the elongation of the hypocotyl lifts the cotyledons from 1 to 3 cm. above the ground level, depending upon the age of the plant at the time of cutting. Cuttings so treated produce from two to five adventitious roots at the lower limits of the hypocotyl, even when it is severed very close to the cotyledons. Cuttings of the epicotyledonary internodes, treated in a similar manner, also produce adventitious roots.

In the hypocotyl, the roots are usually initiated by a general activation of the cells of the V-shaped rays of parenchymatous

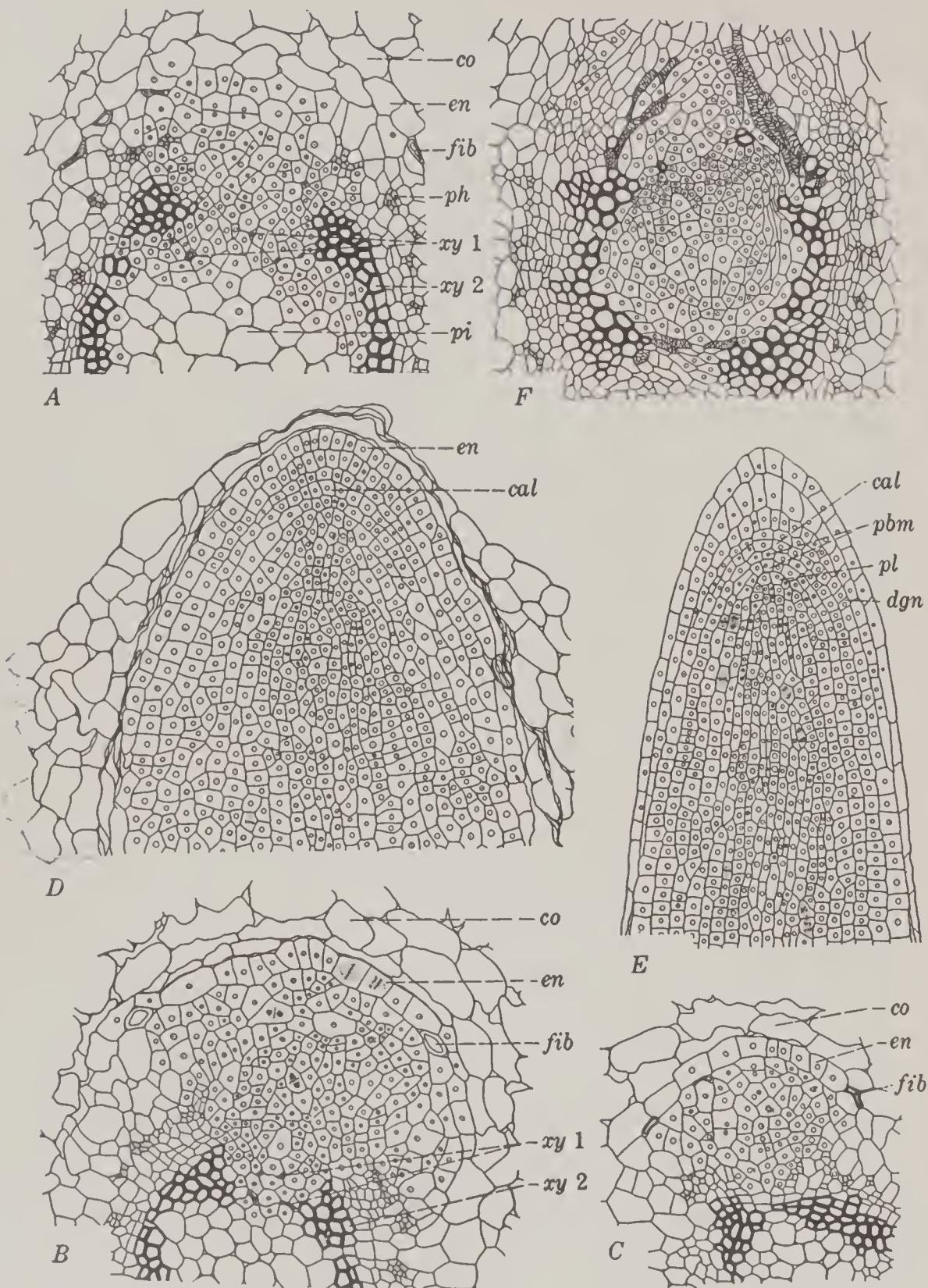


FIG. 207. *A-F*, stages in development of adventitious roots from cuttings of hypocotyl. *A*, *B*, and *D*, initiation of roots in ray parenchyma on same radius as protoxylem; *C*, initiation of root in pericycle and phloem parenchyma not on radius with protoxylem; *E*, median longisection of adventitious root with histogens established; *F*, transection of hypocotyl, median through an adventitious root, showing cell activity throughout pith region: *cal*, calyptra; *dgn*, dermatogen; *en*, endodermis; *fib*, fiber; *pbm*, periblem; *ph*, phloem; *pi*, pith; *pl*, plerome; *xy 1*, primary xylem; *xy 2*, secondary xylem. (After Crooks.)

tissue which extend outward from each protoxylem strand, and the roots arise in two rows, each of which lies in the vertical plane of the cotyledons. In some cases, the meristematic activity extends from the outermost layer of the pericycle centrad to the parenchymatous cells adjacent to the primary xylem. (Fig. 207, A.) Most of the primary xylem elements are crushed and disintegrate as this activity proceeds, and the pith parenchyma may be involved in the process of adventitious root formation. Cell divisions occur in all planes, and a dome-shaped root primordium is formed which pushes outward into the cortical region. The endodermis becomes active, undergoing radial cell divisions, keeping pace with the subsequent growth of the underlying cells. (Fig. 207, B.) It maintains itself as a single layer, and persists over the root cap of the adventitious root until it has grown 1 or 2 mm. into the soil.

No organized histogens can be observed until about the time that the root emerges from the cortex, when the cell layer adjacent to the endodermis begins to divide periclinally, and functions as a calyptrogen. (Fig. 207, D.) The periblem and plerome are clearly defined by the time the root has grown 2 or 3 mm. in length, and the dermatogen is derived from the calyptrogen which functions as a dual layer in the manner described for the primary root. (Fig. 207, E.) Coincident with root formation, cell divisions frequently occur throughout the medullary region of the hypocotyl, forming a continuous cylinder of parenchymatous cells which may remain active for a month or more after the new roots develop. (Fig. 207, F.) This activity of the pith is more pronounced when two adventitious roots develop at the same level, and some tracheids may differentiate in the meristematic region.

Less frequently, adventitious roots may form as a result of general cell activity in the pericycle and phloem parenchyma, in which case they are not in the same vertical plane as the cotyledon. (Fig. 207, C.) Crooks has shown that adventitious roots may also arise from severed cotyledons when they are placed on the surface of moist soil. About 90 per cent of the cotyledons taken from plants 10 days old developed from three to six adventitious roots, and a few cotyledons from 20-day-old plants also produced roots under similar conditions. The cotyledons develop an extensive root system and enlarge somewhat, being thicker than those which are not removed from the plant axis; but they do not produce adventitious buds, although they live for 60 days or more as com-

pared with a longevity of approximately 30 days when they remain on the plant axis. The roots usually originate adjacent to each of the three veins of the cotyledon and as many as three roots may develop near one vein. They push through the adaxial portion of

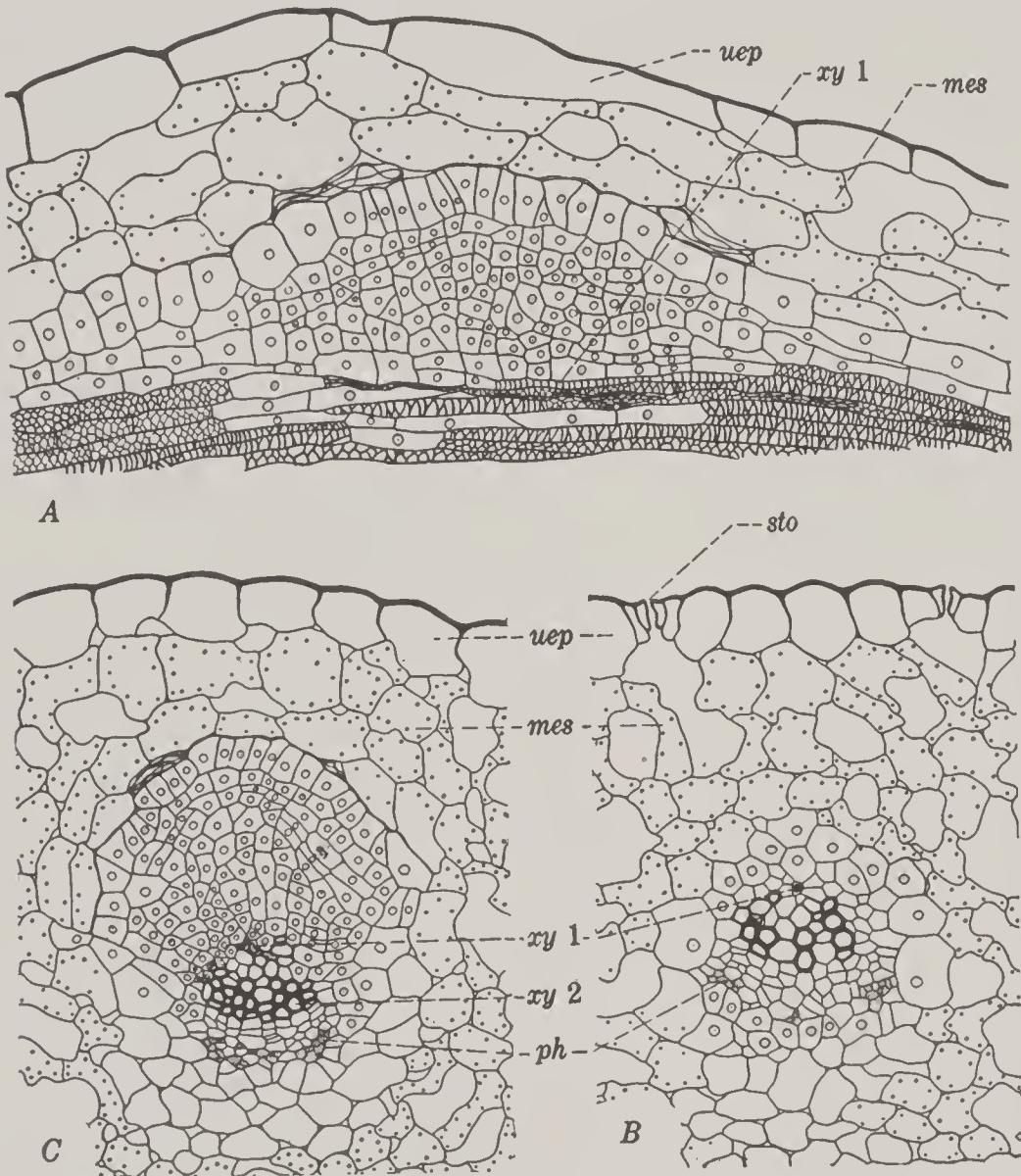


FIG. 208. *A*, longisection through median vein of cotyledon showing origin of adventitious root on adaxial side of bundle; *B*, transection of cotyledon showing development of adventitious root; *C*, transection of cotyledon showing later stage in development of adventitious root: *mes*, mesophyll; *ph*, phloem; *sto*, stoma; *uep*, upper epidermis; *xy 1*, primary xylem; *xy 2*, secondary xylem. (After Crooks.)

the mesophyll of the cotyledon; but may emerge from the cut surface 3 to 4 mm. distant. The primordia are initiated by an activation of a layer of parenchymatous cells surrounding the vascular bundle. (Fig. 208, *B*.) The meristematic region usually extends a millimeter or more along the bundle, producing a dome-shaped group of cells on the adaxial side of the vein, and the subsequent

development of the roots is similar to the adventitious roots of the hypocotyl. (Fig. 208, A, C.)

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CHAPTER XIV

MALVACEAE

GOSSYPIUM spp.

COTTON, *Gossypium* spp., is the chief fiber crop of the world. There are several commercial species in the genus, the number ranging from 29 to 40, depending upon the classification followed. These have been divided into two main groups, the New World cottons which include the Upland and Sea Island varieties, characterized by a $\frac{3}{8}$ phyllotaxy; and the Old World cottons, among which are *G. herbaceum*, *G. arboreum*, and others having a $\frac{1}{3}$ phyllotaxy.

According to Brown (9), the three important species represented in the United States are *G. barbadense*, *G. peruvianum*, and *G. hirsutum*. From these, and very probably from others, many varieties have been derived by selection and hybridization. The number of varieties in cultivation fluctuates since new hybrids are constantly being developed on the one hand, while the use of others is discontinued for some reason or other. In 1927, Brown listed 75 varieties of Upland cotton, stating that the list was not to be considered complete or exhaustive, as he had included in it only the "most prominent old-time varieties, some varieties from which common everyday varieties have sprung, and the leading varieties being grown at present." Duggar (13), some years earlier, stated: "It is probable that the number of distinct varieties, each differing from the other in one or more items of botanical importance, exceeds one hundred." He simplified the classification greatly by dividing the American Upland, short-staple cotton into six classes, to which he added a seventh class with intermediate staple, and an eighth group including all the long-staple varieties.

GENERAL MORPHOLOGY

THE SHOOT. — In the wild state, cotton is a perennial with a shrubby or tree-like habit; but, in cultivation, it grows as an herbaceous annual or biennial. In Upland varieties, the main

stems are erect or somewhat branching, and may attain a height of 2 to 6 feet. (Fig. 209.) In the native, tropical home of cotton, some of the tree-cottons reach a height of 15 to 20 feet. The



FIG. 209. Cotton plant showing branching and inflorescence. (Photograph by Harrold.)

leaves are petiolate, roughly cordate, three to nine lobed, and usually palmately veined; but there are great differences in size, shape, texture, and degree of pubescence. The basal stipules are for the most part deciduous. The plants are conspicuously glandular, large glands occurring on the abaxial surface of the leaves, on

the bracts, petioles, stems, and the embryo, especially its cotyledons. Floral nectaries occur at the base of the inner surface of the calyx, and there are three sets of extra-floral nectaries located on the leaf, and on the outer and inner surfaces of the involucral bracts.

The primary axis consists of two types of branches. The main stem is indeterminate with a terminal growing point, while the lateral branches arising in the axils of the leaves of the main stem are of two kinds, one type being vegetative and the other fruiting. The vegetative branches are similar in function and morphology to the primary axis, but the fruiting branches are distinctive in form, function, and mode of development. In the axil of each leaf there are two buds, one of which may be rudimentary. The true axillary bud is centrally located above the middle of the base of the petiole, while the lateral or extra-axillary bud is to the right or left of the axillary bud. These two buds differ with respect to their further development, the axillary bud producing only vegetative branches or "limbs," while the branches which bear flowers and fruit are developed from the extra-axillary one. (Fig. 210.)

There is some variation with respect to the axillary and extra-axillary or accessory bud development in the several varieties of cotton, and in some instances, a single bud may occur in the axil of the leaf. According to Templeton (34), there is a bud in the axil of each cotyledon in Egyptian cotton which does not develop, and each of the other leaves has a true axillary and an accessory bud. In the usual development of the plant, only one of the two buds in a given axil develops into a branch. Normally, at the first three or four nodes above the cotyledons, the axillary buds develop and the extra-axillary buds remain dormant, so that a zone of vegetative branches is formed in which the branches resemble the main axis in the development of nodes, leaves and axillary buds. Above the fourth or fifth node, only the extra-axillary buds usually develop, forming a zone of fruiting branches. There may be a third or transition zone between the vegetative and fruiting zones in which the buds are irregular in their behavior. In this zone, both buds may become active, both may abort or remain dormant, or either one of the two may develop. When the vegetative branch develops, the phyllotaxy is the same as that of the main axis; and the axillary buds may give rise to fruiting or to

new secondary branches. Near the top of the main stem, both buds may develop; and when this occurs, the axillary buds produce new sympodia or single flowers; and the extra-axillary ones fruiting branches.

The fruiting branches that develop from the extra-axillary buds assume a nearly horizontal position, rather than the vertical or ascending one of the vegetative bud. The first internode of



FIG. 210. Sympodial branching in cotton. The plant was pruned in such a way that both axillary and extra-axillary buds developed. (Photograph by Doak.)

the fruiting branch is long; and, at the second node, a leaf arises with two basal stipules which almost completely encircle the node. The floral bud appears to arise approximately opposite the point of divergence of this leaf rather than from its axil. Gore (18) describes this situation,

"Examination of a fruiting branch shows that the flowers are not in the axil of a leaf, but appear to stand opposite the adjacent leaf. The internodes of this branch are slightly zigzag and the leaves appear as if alternately arranged. . . . Such a sympodium is developed more or less as follows: from the axil of a leaf on a given axis, there arises a new axis which by its growth pushes the terminal portion of the axis from which it arose to one side so that this once terminal portion may come to appear as if lateral in origin."

The axillary bud may develop in the usual fashion, producing a vegetative branch, or it may produce a short vegetative branch which will in turn produce fruiting branches. The development of a short vegetative branch producing fruiting branches gives it the appearance of a fruiting branch bearing several flowers or bolls; but, actually, only one is borne on each branch. The leaves on the fruiting branches do not have the same arrangement as those on the main axis owing to the sympodial method of branching and the twisting of the joints of the fruiting branches, which orients the flower buds in an upright position and aligns the alternate leaves in two rows.

THE ROOT. — The plant develops a tap root which penetrates the soil for 2 feet or more under favorable conditions. With irrigation, Balls (6) records a penetration of about 7 feet in one of the Egyptian varieties, and King (23) reports a tap root of the Pima variety grown in Arizona that reached a depth of nearly 11 feet, noting that "a considerable number of secondary roots extended to great depths and apparently shared the function of the tap root." He also observed a relation between extent of the root system and "water stress"; stating that

"Plants which had produced the greatest quantity of vegetative growth appeared to suffer most frequently from 'water stress' remaining longer in a wilted condition between irrigations and showing an earlier recurrence of wilting after irrigation. The fact that there was no appreciable difference in size or distribution between roots of large plants and small plants seems to indicate that a limiting root system may have an important bearing on the water-stress behavior of the largest plants."

The depth and extent of the lateral root system depend upon soil moisture; but, in general, it is shallow, and the laterals originate 2 to 6 inches below the soil surface, although they may be even more shallow under very moist conditions. The radial extent of the laterals may approximate 4 feet, and they branch and rebranch so that the first few inches of surface soil is well filled with roots. In some instances, a second system of laterals may develop at lower levels when the tap root reaches saturated soil.

The secondary roots arise in four or five shallow longitudinal grooves that may be somewhat spiral owing to the torsion of the root, and subterranean shoots sometimes arise in the depressions adjacent to the roots. According to Cook and Meade (10),

"the underground shoots have at first a rounded or irregular form, like root nodules or galls, and may represent modified root primordia. The nodules grow to various sizes, sometimes attaining a diameter of nearly an inch before showing the leafy bud that develops into a vegetative branch. . . . Subterranean shoots seem to be developed much more freely in the Egyptian cotton than in Upland varieties."

THE FLOWER AND FRUIT. — The flowers are convolute in the bud, and are usually white or yellowish although they may be deep yellow at anthesis or even a brilliant red in some foreign varieties. In some of the white-colored forms, there may be a spot of purple on the claw of the petal. The first day after anthesis, the corolla becomes pink and turns red the second day. At the end of the third day, it withers and falls off, together with the staminal column, the stamens, and the stigmas, while the ovary remains, subtended by the calyx and covered by the persistent involucre.

The somewhat bell-shaped flowers are large, regular, hypogynous, and tetracyclic. The persistent calyx consists of five undivided sepals that form a shallow cup around the base of the petals, and its lobes are variable in size, being short and broad, or somewhat long and pointed. As the boll develops, the calyx becomes tightly adherent to its base. The sepals have a large number of globular subepidermal glands that occur in irregular rows in the parenchyma between the vascular bundles. Within the calyx and alternate with its lobes, greenish spatulate or obovate organs may be frequently found. They are usually five in number, and may be very small and rudimentary, or, in some instances, large enough to extend to the margin of the calyx. Cook and Meade

(10) have interpreted them as "ingrown margins of the calyx lobes" or "stipular elements." Centrad to and at the base of the sepals is a ring of nectaries made up of multicellular glands which are surrounded by stiff hairs.

The tubular corolla consists of five obcordate petals with lobes that alternate with those of the calyx, and each glandular petal overlaps the next one in the series in a convolute manner. The stamens are numerous, there frequently being as many as 90 or 100. These are diverged from a tubular sheath of tissue, or staminal column, which completely surrounds the pistil except for the projecting stigmas and a short portion of the style. (Fig. 211.) The filaments appear to arise in five fascicles or groups, but close examination shows that there are actually ten fairly well defined groups of stamens arranged in more or less vertical rows. The anthers are bilocular, and dehisce along a single line running over the crest of the anther, liberating large, spinose pollen grains.

The pistil consists of from three to five undiverged carpels, and the three- to five-loculed or "locked" boll is a dehiscent capsule that splits along the dorsal sutures. In a given variety, the number of carpels may vary within the limits noted above even on an individual plant. In Upland cotton, the four- to five-locked bolls are more common than the three-locked ones, and two-locked types occur in Egyptian cotton. Abnormal cases have been reported in which six or more carpels may occur. The boll is thick and leathery at maturity and is usually subglobose or oval in shape. (Fig. 212.) In each locule, eight to ten ovules arise in two parallel rows, and ultimately the seeds produce the commercial fiber.

The flower is subtended by an involucre composed of three, or occasionally four, unequal, leaf-like bracts. These are ridged,



FIG. 211. Median longisection through flower. *A*, staminal column; *B*, base of corolla tube; *C*, ovary; *D*, bract of involucre. (Photograph by Doak after Balls.)

deeply notched with about ten teeth which correspond to the principal veins. On their outer surfaces, characteristic stellate hairs are developed along the ridges formed by the vascular bundles. Bracteoles may occur inside of the involucre alternating with the



FIG. 212. Habit of mature bolls. (Photograph by J. Horace McFarland Co.)

bracts. Frequently, only two are present; and, in this case, they are located on either side of the small bract.

ANATOMY

THE SEED. — The seeds are irregularly pear-shaped, ranging in length from $\frac{1}{4}$ to $\frac{1}{2}$ inch, and they are usually covered with fibers of two kinds, the commercial fiber or "lint" and the "fuzz"

or short hairs. When the lint and fuzz are completely removed, the naked seed is black or dark brown. In some varieties, no fuzz is produced and the seed is left naked after ginning. In Upland cotton, the two kinds of hairs are mixed together over the whole surface of the seed; but, in some varieties, the lint tends to have longer fiber at the rounded end than at the pointed one. The lint is usually white while the fuzz is frequently greenish, brownish, or tawny.

The seed coats are developed from two integuments and have been described in detail by Winton (36). The outer epidermis, aside from the fiber cells or hairs, consists of cells which are irregular in shape. In surface view, they are somewhat stratified, with yellow walls and dark brown contents. They form rosette-like groups around the hairs and vary in size from 10 to 60 μ . Stomata with thin, translucent-walled guard cells occur either singly or in pairs. The hypodermal layer is two to three cells in thickness, except in the region of the raphe where it is thicker, and consists of thin-walled cells with irregular contour and brown pigmentation that may become more or less compressed or crushed. Inside this zone is the innermost layer of the outer integument comprised of rather thick-walled, colorless cells. (Fig. 213.)

The palisade cells constitute approximately one-half of the thickness of the seed coat. These elongated cells are very characteristic in structure, consisting of an outer portion occupying about one-third of the length of the cell with nearly colorless walls, and an inner portion with yellowish-brown walls. In the outer portion of each cell, the lumen is very narrow except for a globular enlargement at the inner end which contains a dark-colored substance. The inner portion appears to have no lumen when viewed in cross section; and, in the tangential view, radiating lines may be seen which probably result from the arrangement of the lamellae of the cell wall. The inner brown coat consists of several compressed layers of more or less spongy polygonal cells which contain a brown coloring matter such as is found in the outer brown coat.

Within the inner brown coat is a delicate white sheath two cell-layers in thickness which encloses the embryo. The cells of the outer layer were designated as "fringe cells" by Hanausek (20), who regarded them as the remains of the perisperm or nucellus, and a similar interpretation was made by Winton (36) and

Balls (4). Reeves (27) has reached a different conclusion with respect to this layer, on the basis of comparative studies of young ovules; and states that "the fringe tissue originates as the inner epidermis of the inner integument." The cells are polyhedral, and the walls are irregularly thickened or fringed so that they appear to be nodular or wavy. The second layer of the sheath consists of thick-walled cells containing aleurone grains which

are the remains of the endosperm. The cotyledons are thrown into complicated folds in their development; but, when straightened out, are broad and kidney-shaped. They contain very prominent resin cavities and reserve foods, including aleurone and fat from which cotton seed oil is derived.

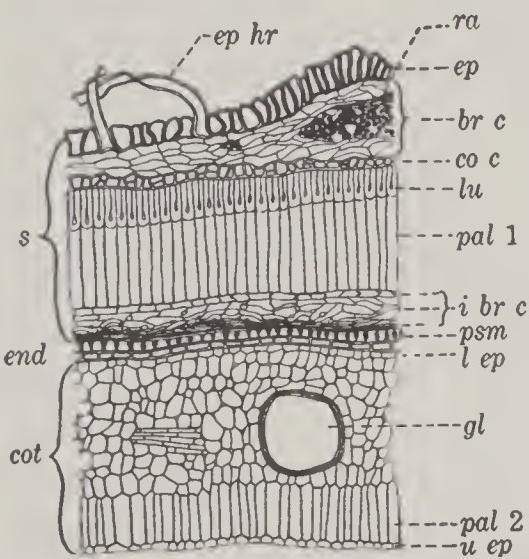
DEVELOPMENT OF THE SEEDLING.

— The cotton seedling develops rapidly and the primary root pushes its way through the micropyle of the seed and grows without branching for several days. Measurements by Balls (6) indicated a growth in length of 6 cm. in the first four days, and an additional 8 cm. in the ensuing three days. During this time, there is a prolific development of root hairs in the region above the zone of elongation. The straightening of the arched hypocotyl lifts the much

FIG. 213. Section of seed including seed coat, perisperm, endosperm, and cotyledon: *br c*, outer brown coat; *co c*, layer of colorless cells; *cot*, cotyledon; *end*, endosperm; *ep*, epidermis; *ep hr*, epidermal hair; *gl*, gland; *i br c*, layers of inner brown coat; *l ep*, lower epidermis of cotyledon; *lu*, lumen of palisade layer of seed coat; *pal 1*, palisade cells of seed coat; *pal 2*, palisade cells of cotyledon; *psm*, perisperm consisting of fringe cells; *ra*, raphe; *s*, seed coat; *u ep*, upper epidermis of cotyledon. (After Winton and Winton, *Structure and Composition of Foods*, John Wiley and Sons, Inc.)

convoluted cotyledons out of the ground; and after being freed from the seed coats, they expand rapidly. Coincident with this development, lateral root formation occurs, and subsequent growth of the epicotyl results in the elongation of the axis and the production of the first foliage leaves. (Fig. 214.)

THE PRIMARY ROOT. — The primary root has an exarch, radial protostele which is generally tetrarch, although pentarch primary roots may occur. (Figs. 215 A, 216.) The protoxylem is composed of spiral and annular elements that become much elongated



as the axis matures, with the result that the spiral thickenings become longitudinally stretched, and the thin walls frequently collapse. The metaxylem develops centripetally, consisting of scalariform and scalariform-reticulate elements. At the center of the stele, there are four to eight large tracheae which are sometimes separated by smaller xylem elements with scalariform thickenings. Complete maturation of the centrally located elements does



FIG. 214. Stages in development of seedling.

not occur until about the time that secondary thickening is initiated.

On alternate radii to the protoxylem are four groups of primary phloem that are separated from the central metaxylem elements by parenchyma. The protophloem is parenchymatous and is soon crushed, while the metaphloem consists of sieve tubes, companion cells, and parenchyma. As the maturation of the primary axis proceeds, some of the phloem cells adjacent to the cambium initials become thick-walled, and sieve tubes and companion cells are located at the lateral edges of these groups. (Fig. 215, A.) The thin-walled, elongated cells of the pericycle form a single layer external to the phloem region, but this region may be two or three cells in thickness outside the protoxylem elements.

The endodermal cells form a single layer with well-defined

Casparian thickenings, and those abutting the phloem groups are filled with a mucilaginous substance that is lacking in those adjacent to the protoxylem. The cortical parenchyma is spongy,

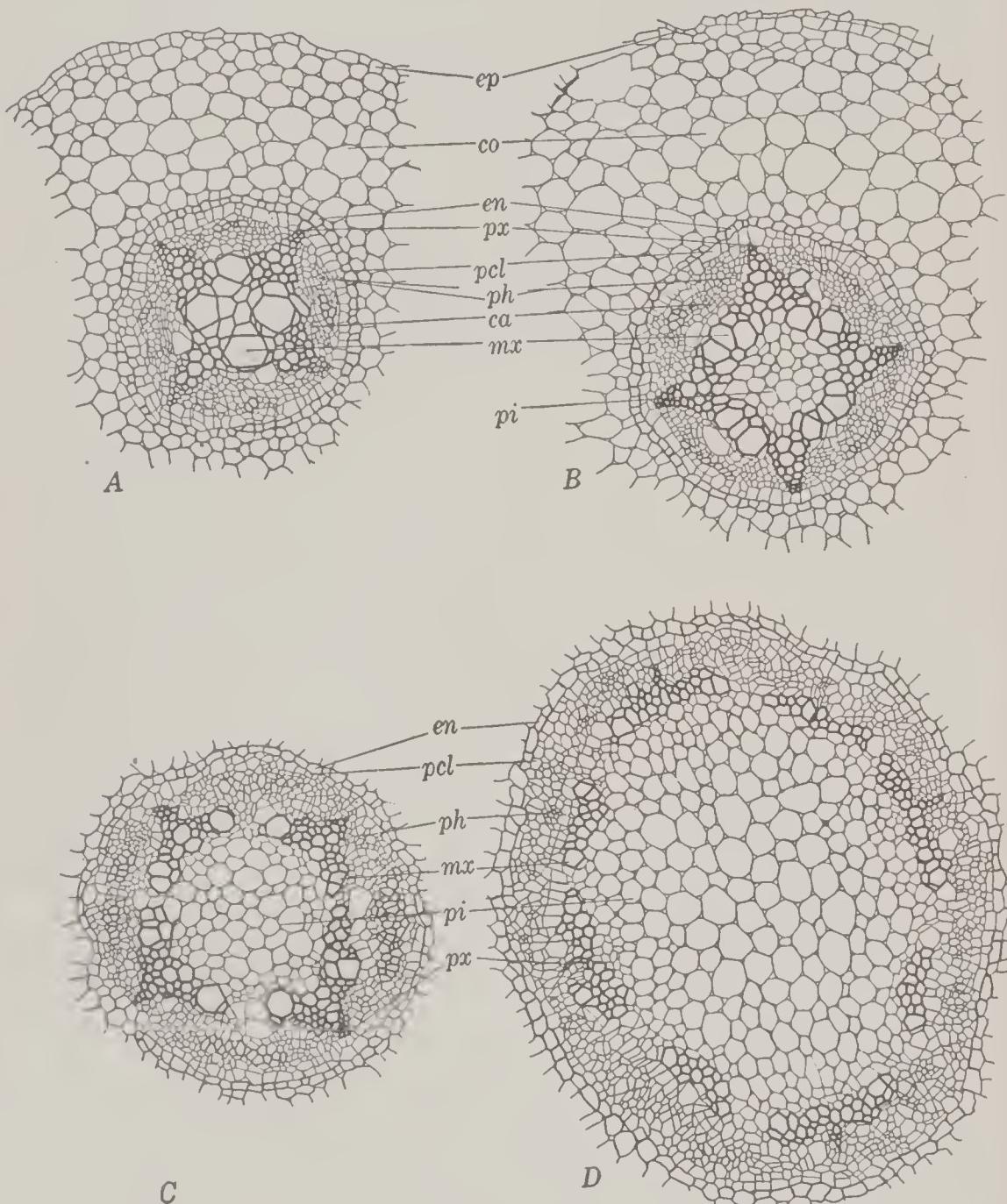


FIG. 215. *A*, transection of primary root; *B* and *C*, of lower hypocotyl; *D*, of middle hypocotyl: *ca*, cambium; *co*, cortex; *en*, endodermis; *ep*, epidermis; *mx*, metaxylem; *pcl*, pericycle; *ph*, phloem; *pi*, pith; *px*, protoxylem. (After Spieth.)

consisting of eight to twelve concentric layers of thin-walled, isodiametric cells except for the two or three rows immediately within the epidermis, which are axially elongated and more compact. The epidermis consists of a single layer of small cells.

SECONDARY THICKENING OF THE Root. — Secondary thickening begins early in ontogeny and the first cambial activity occurs in the zone of fundamental parenchyma lying between the central metaxylem vessels and the primary phloem. The secondary xylem consists of large vessels, smaller conductive elements, fibers and parenchyma. The parenchyma forms rays that are one to three or more cells in width, and the thin-walled ray-cells are radially elongated. The large vessels are laid down in radial rows, but become somewhat irregular in arrangement owing to the increase in their size. Frequently, two or more of these large vessels are clustered together, but the major portion of the xylem consists of smaller vascular elements, fibers, and the thin-walled parenchyma which surrounds the large vessels.

Outside of the cambial zone, the secondary phloem has a characteristic layered appearance which results from the differentiation of zones of small, thick-walled phloem fibers that alternate with regions of sieve tubes and companion cells. In some instances, the fibers occur in compact groups rather than in layers. The wedge-shaped segments of fibers and sieve tubes are separated from each other by funnel-shaped zones of ray cells. In most cases, these are secondary phloem rays that are continuous centripetally with the secondary xylem rays; but in less frequent instances where they are not produced by cambial activity, they may be regarded as being pericyclic in origin. As the root increases in size, the cortical and epidermal cells are stretched and ultimately disintegrate; but the pericycle remains active during the secondary

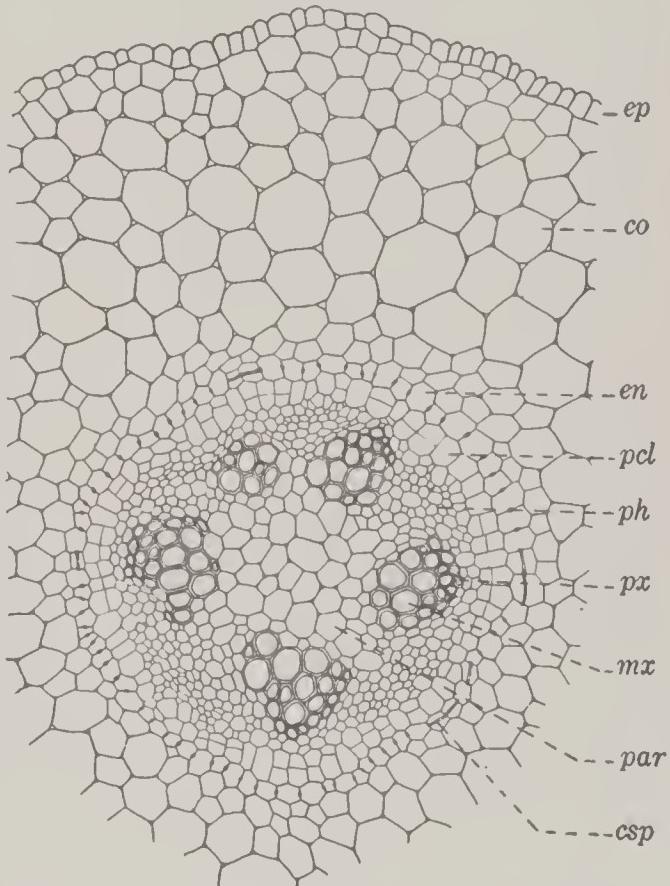


FIG. 216. Transection of young pentarch root: *co*, cortex; *csp*, Caspary strip; *en*, endodermis; *ep*, epidermis; *mx*, metaxylem; *par*, parenchyma; *pcl*, pericycle; *ph*, phloem; *px*, protoxylem.

phases of growth, producing a multilayered periderm that serves as a protective zone for the mature root.

THE VASCULAR TRANSITION. — The vascular transition in the seedling axis has been investigated by Spieth (32), who used five-day-old seedlings. In a hypocotyl of this age, the primary vascular tissues of the lower portion are completely differentiated and secondary thickening initiated; but, in the upper limits of the same hypocotyl, the maturation of the primary tissues is just beginning, there being little differentiation of vascular elements at the cotyledonary node. The immature condition of the upper hypocotyl and the cotyledonary node as compared with the middle and lower hypocotyl is due to the fact that the former is a region of continued axial elongation resulting from the activity of an intercalary meristem.

The first evidence of change in the vascular plan occurs in the lower hypocotyl, about one centimeter below the soil surface, in connection with the differentiation of the metaxylem. Instead of forming a central strand, it differentiates in a ring surrounding centrally located parenchymatous cells which are circular in transection and vertically elongated with intercellular spaces at their angles. (Figs. 215, *B*; 219, *B*.) The phloem groups are more extensive at this level and one or two rows of phloem cells immediately inside of the pericycle have thick walls. Sieve tubes and companion cells differentiate laterally in relation to the thick-walled phloem cells, and adjacent to the protoxylem points.

Just above this level, the stele enlarges within a very short vertical distance, and four triangular groups of primary xylem cells are differentiated. (Figs. 215, *C*; 219, *C*.) Each group consists of protoxylem at the outer apex of the triangle, and two tangentially oriented arms of metaxylem which lie in an approximate collateral position with reference to the primary phloem. At a higher level, parenchyma is differentiated between the metaxylem arms so that the four distinct groups of primary xylem are separated from each other by medullary rays. Further differentiation results in the formation of tangential bands of metaxylem that alternate with the four transition bundles. (Figs. 215 *D*; 219, *D*.) The position of the four principal phloem groups remains unchanged, except that there is a large number of thick-walled phloem cells adjacent to the pericycle, and small groups of sieve tubes and companion cells are scattered among these thick-walled elements.

About 2 cm. above the soil level, the xylem of each of the four original transition bundles consists of two rows of spiral elements and two lateral metaxylem arms. (Fig. 217, A.) The cambium is active and there is considerable secondary thickening which results in the differentiation of secondary xylem adjacent to the

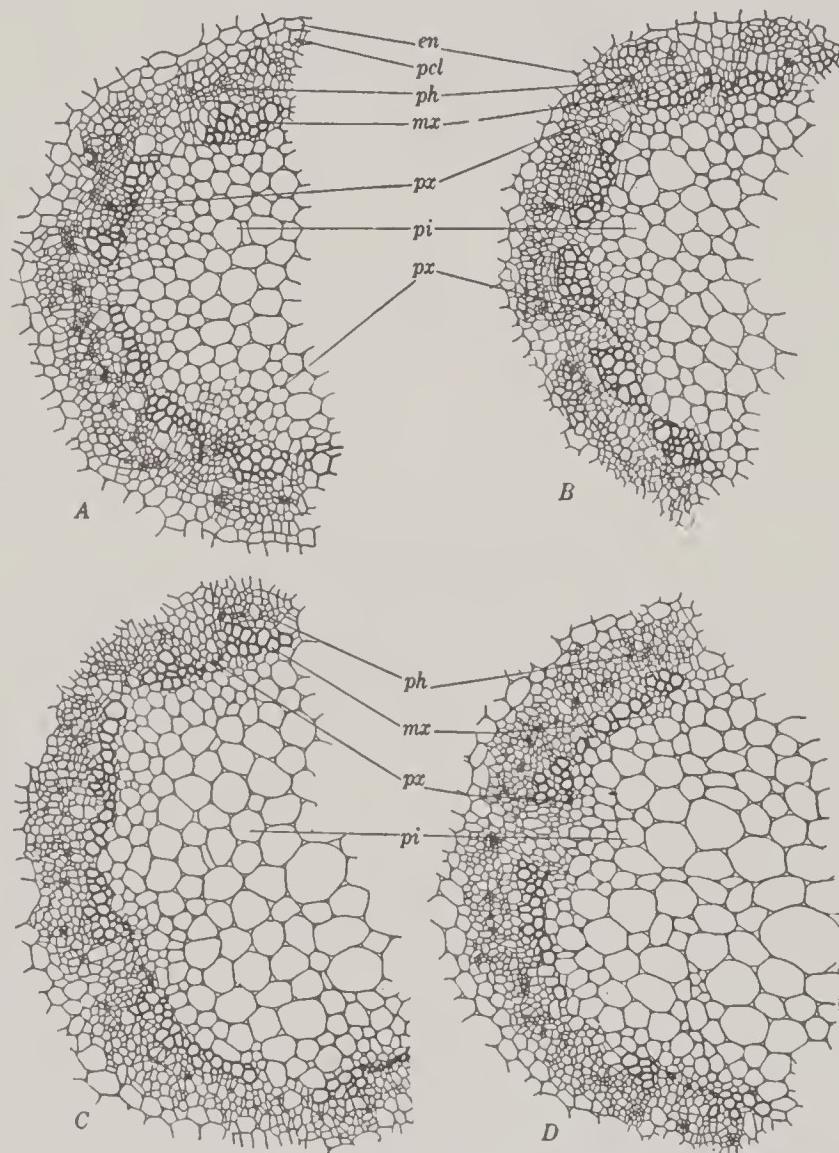


FIG. 217. A-D, successive stages showing transition in upper hypocotyl: *en*, endodermis; *mx*, metaxylem; *pcl*, pericycle; *ph*, phloem; *pi*, pith; *px*, protoxylem. (After Spieth.)

tangential rows of metaxylem. Secondary phloem is laid down centrifugally, the endodermis and the pericycle maintaining their continuity by anticlinal divisions. The cortex is composed of fifteen or more concentric layers of cells, and lysigenous canals may develop in the outer portion of this region.

At approximately 4 cm. above the level where transition is initiated, the separation of each bundle into two units is completed. Except over the protoxylem points, where the tissue

remains parenchymatous, thick-walled pericyclic cells abut the endodermis, which becomes discontinuous, retaining its identity only over the transition bundles. (Figs. 217 B; 219, F.) Secondary xylem and phloem are formed except outside the protoxylem points where parenchymatous rays occur. The protoxylem points of the divided transition bundles occupy a position more in line with the metaxylem cells so that the primary xylem arms are tangentially oriented.

Somewhat higher in the hypocotyledonary axis, there is a definite decrease in cambial activity, and the phloem is arranged in smaller groups separated from one another by parenchymatous cells. (Fig. 218, A.) At successively higher levels, the progressive differentiation of the protoxylem in a more centripetal position, and of the metaxylem in a centrifugal one, results in an endarch orientation of the primary xylem tissues. (Fig. 218, B.) This reorientation is gradual, but eventually the endarch arrangement is reached in all bundles. The parenchymatous rays, separating the halves of the original transition bundles, become progressively wider; and there is evidence of the meristematic character of the hypocotyl at this level in the relatively small number of mature metaxylem elements. The sieve tubes and companion cells lie in a collateral position external to the four pairs of transition bundles, but there are no thick-walled cells in the phloem.

About 8 cm. above the soil surface, the rays that bisect the transition bundles lying in the intercotyledonary plane widen to such an extent that one-half of each bundle lies on either side of the hypocotyledonary axis. (Fig. 219, G.) Thus, four units of the original transition bundles are located on each side of the axis. Each group consists of one original transition bundle in which the two units are separated by a narrow ray, and one unit from each of the transition bundles of the intercotyledonary plane, the bundles $a'd'd'c'$ and $a'b'b'c$ constituting the left and right cotyledonary traces respectively. (Fig. 219, H, I.) In the intercotyledonary plane, there are from one to three endarch bundles which in this stage of development consist of a few primary xylem and phloem elements. (Fig. 219, J.)

At the cotyledonary plate, the four bundles of each trace diverge into their respective cotyledons. The endarch bundles are the downwardly diverging strands of the traces of the foliage leaves above. Ultimately they become continuous with the cotyle-

donary vascular system by anastomoses, and by the development of secondary vascular tissues as the node and upper portions of the hypocotyl mature.

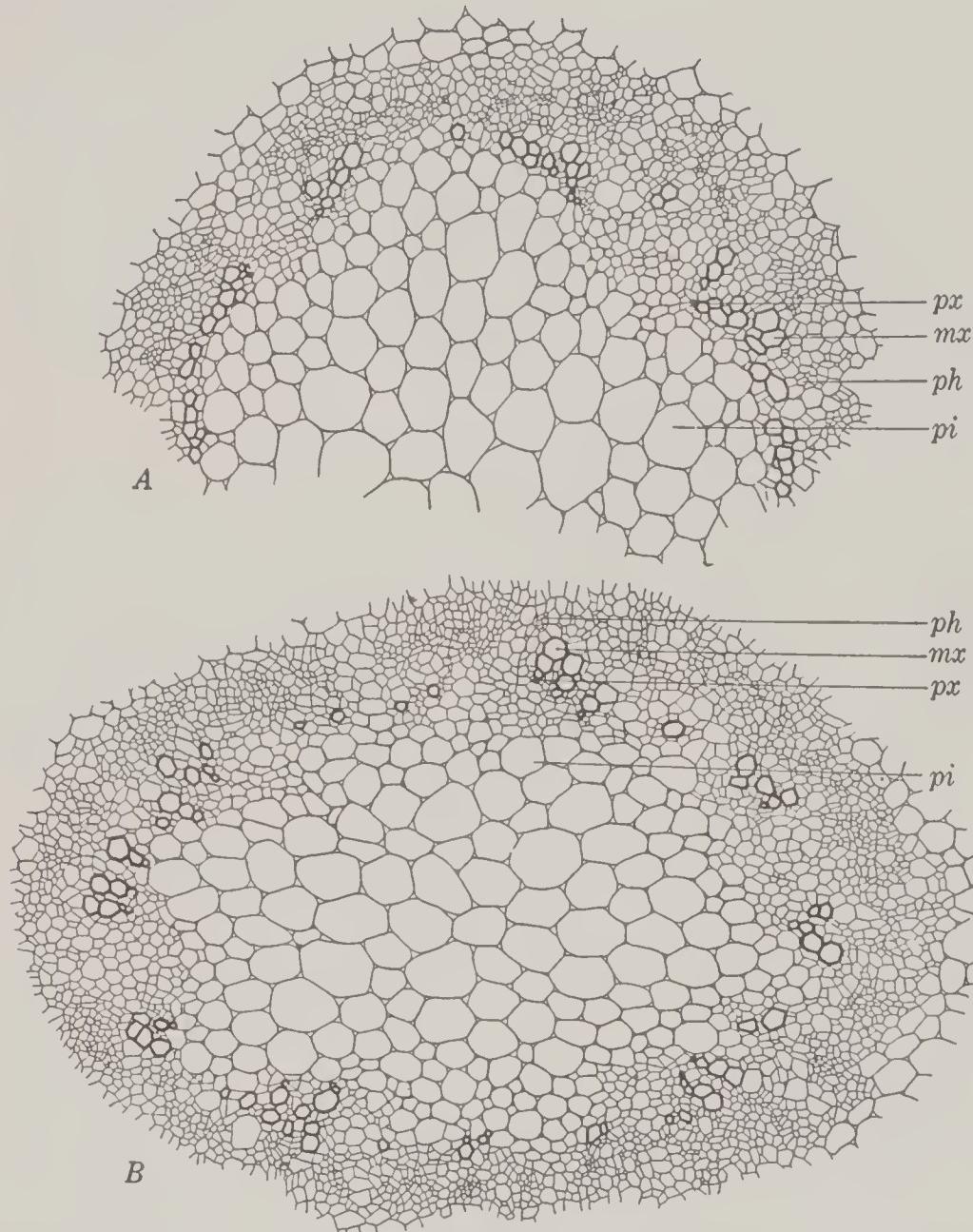


FIG. 218. *A* and *B*, transections of upper hypocotyl showing stages in transition at level where endarch condition is attained: *mx*, metaxylem; *ph*, phloem; *pi*, pith; *px*, protoxylem. (After Spieth.)

ONTOGENY OF THE FRUITING BRANCH. — The development of the main stem and its vegetative branches results from the continued activity of the terminal meristem of each axis. This monopodial growth is in contrast to the sympodial development of the fruiting branch. (Fig. 220, *A*, *B*.) Gore (18) has described the ontogeny of the fruiting axis in detail.

"A single segment of a fruiting branch consists of an internode, a leaf with stipules, the flower bud, and two axillary buds one of which remains dormant and becomes the axillary bud of the fruiting branch while the other continues the secondary axis. The fruiting branch of cotton is made up of a series of these segments which gives to the entire structure a jointed appearance. (Fig. 221, A.) . . . The first evidence of the development of a fruiting branch is a primordium

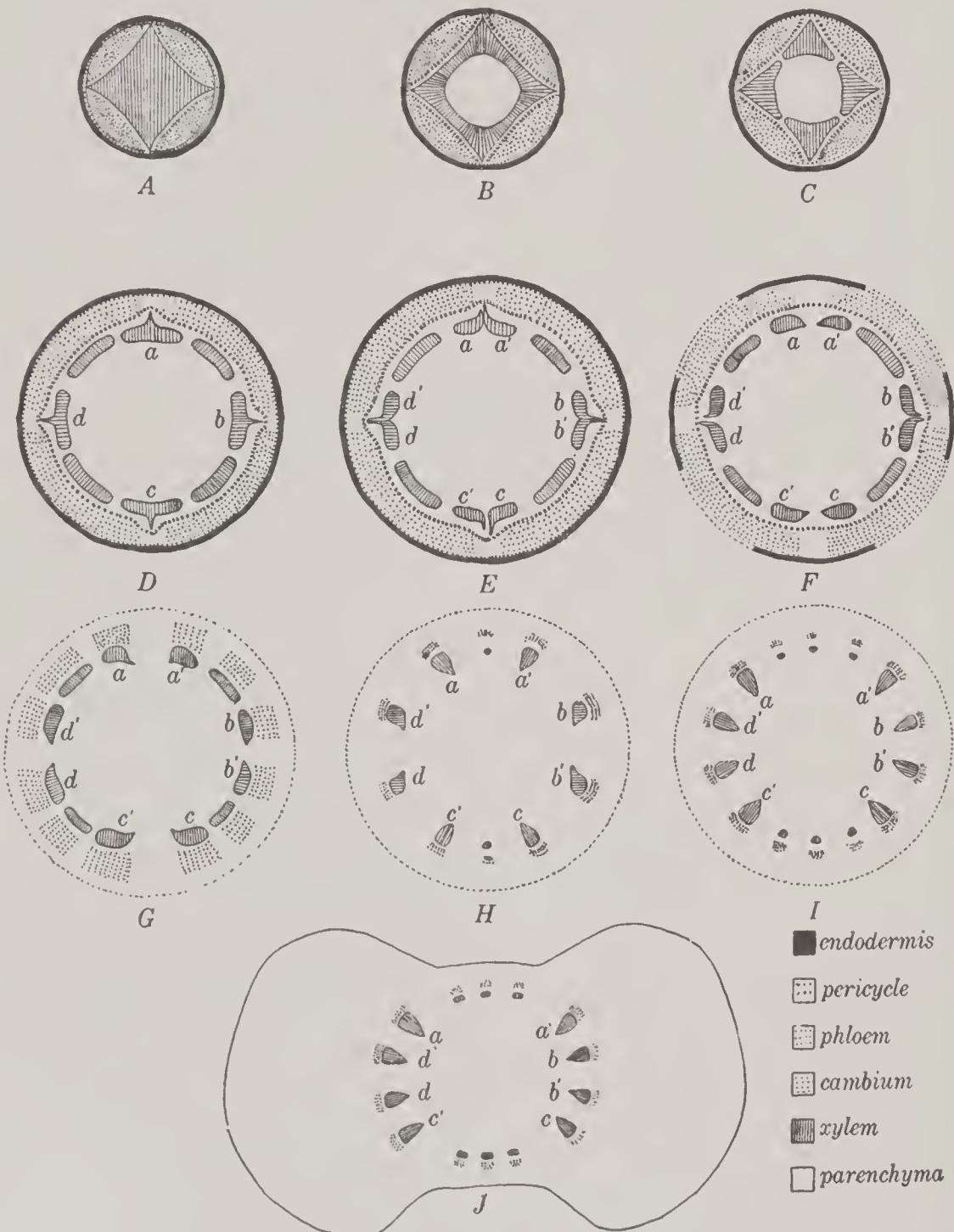


FIG. 219. Diagrams illustrating vascular transition: A, transection at root level; B and C, lower hypocotyl; D and E, middle hypocotyl; F-I, upper hypocotyl; J, cotyledonary node. (After Spieth.)

which occurs in the axil of a leaf on the main stem at the second or third node back from the apical meristem. (Fig. 220, B.) This axial primordium is early differentiated into two separate growing points: one grows faster and becomes the fruiting branch primordium; the other grows slowly and develops the axillary bud on the main axis, which is homologous with the axillary bud of the fruiting branch. The fruiting branch primordium becomes raised at three points where the first leaf and stipules are to arise. At this stage a single primordium exists which resembles the apical primordium of the main stem. After the leaf and stipule primordia are definitely differentiated it begins to grow away from the subtending leaf and is directed away at an increasing angle. It becomes bluntly conical in shape and projects beyond the subtending stipules continuing its development into a

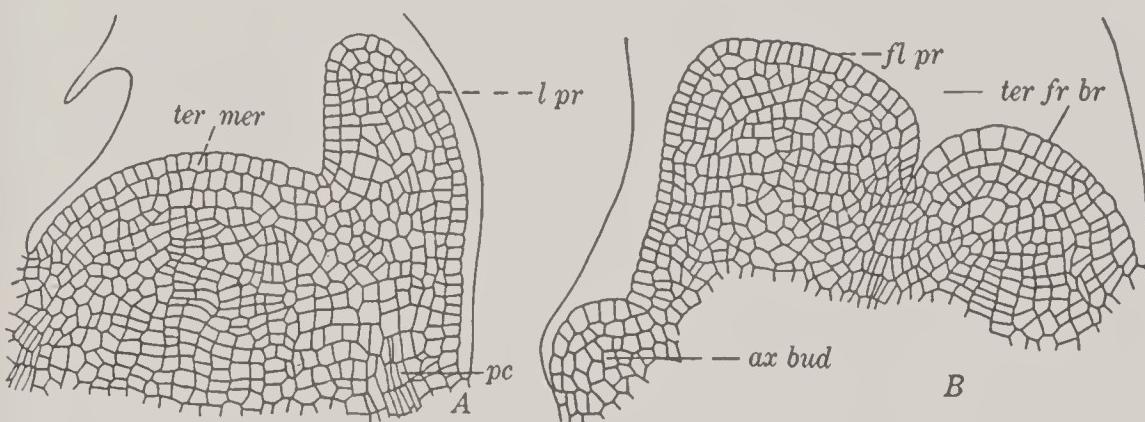


FIG. 220. A, longisection of apex of main axis; B, same of fruiting axis: *ax bud*, axillary fruiting branch bud; *fl pr*, flower primordium; *l pr*, leaf primordium; *pc*, procambium; *ter fr br*, terminal fruiting branch; *ter mer*, terminal meristem. (After Gore.)

flower bud. At this same time a zone of tissue becomes active between the leaf and the primordium of a flower. It soon develops two unequal-sized growing points, the smaller of which gives rise to the axillary bud; the larger one continues the fruiting branch by developing a leaf and stipules for the next axis. By a repetition of this process the fruiting branch comes to consist of a series of axes, each axis made up of a single internode and each terminated by a flower. (Fig. 221, B, C.) Cottons in which a sympodium consists of more than one internode are exceptional. . . . Early in the development of the fruiting branch, when the first fruiting axis is being formed, it is pushed to one side so that the developing structures are projected to one side of the leaf on the main stem. Thus a fruiting branch is more nearly horizontal with the primary axis and grows out either to the right or left of the subtending leaf on the main stem."

DEVELOPMENT OF THE AXILLARY BUD OF THE FRUITING BRANCH. — The development of the bud which occurs in the axil of the leaf on a fruiting sympodium has been reported by King, Cook and Meade, and Gore. Cook and Meade (10) state that

"In addition to the bud that continues the growth, there are buds in the axils of the leaves of the fruiting branches, and if these develop they may produce vegetative branches of the usual form. In other cases the axillary buds of the fruiting branch may produce very short vegetative branches, and these may give rise in turn to very short fruiting branches, so that one joint of a fruiting branch may appear to bear two or three bolls in an exceptionally fertile plant. Careful examination will show that only one boll is borne directly on the joint and that the others come from branches of the short axillary."

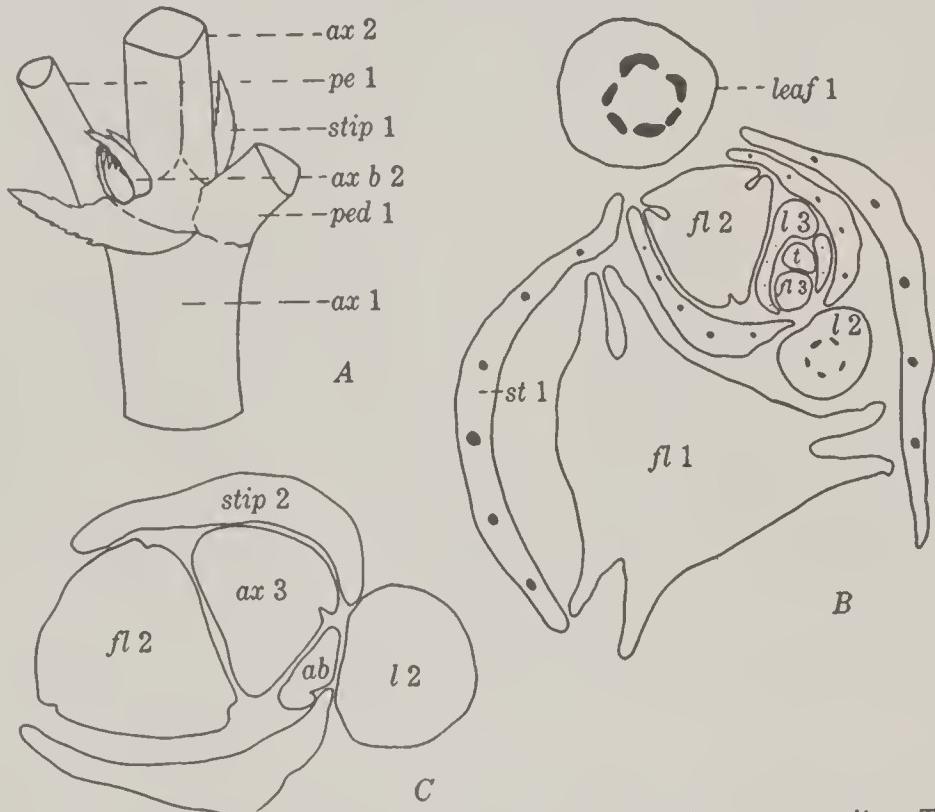


FIG. 221. A, portion of fruiting branch showing parts of two sympodia. The termination of axis 1 is the flower whose pedicel is shown, together with leaf and stipules: *ax 1*, 2, axes 1 and 2; *ax b 2*, axillary bud developed from axis 2; *pe 1*, petiole; *ped 1*, pedicel of flower; *stip 1*, stipule; B, outline of transection of terminal bud of fruiting branch showing three sympodia and terminal of fourth axis (axillary fruiting branches not shown): *fl 1*, 2, 3; *l 1*, 2, 3; *st 1*; and *t*, flowers, leaves, stipule, and terminal for respective sympodia; C, lower level on sympodia 1 and 2 with greater enlargement: *ab*, axillary bud of axis 3, *ax 3*. (After Gore.)

King (24) points out that

"The axillary buds and branches on the fertile branches of Egyptian cotton differ in morphology and behavior from those on upland cotton. In the Pima variety of Egyptian cotton rudimentary axillary branches begin development with the advent of minute triangular buds in the axil of each leaf, but ordinarily this development is cut short by the shedding or drying up of the buds, which maintain active growth for only a few days. In upland varieties the axillary buds usually remain dormant, but they can be stimulated to growth at any time later in the season."

Gore (18) investigated the axillary buds of Pima, Sea Island, and Mebane varieties and describes the development of the latter as follows:

"The first divergence from the axillary bud primordium is a bract-like structure, unattended by stipules, possibly representing a reduced leaf and stipules. There next arise a leaf and stipules for the second node, followed by the turning aside of the growing point and the development of a sympodium. The new terminal primordium develops a monopodial axis at the next node, however, and at a succeeding node another sympodium may be developed. This alternate production of a sympodial axis and a monopodial axis may continue until three or four flower primordia are produced."

ANATOMY OF THE STEM. — The young stem is irregularly three to five lobed or ridged with large bundles lying on the same radii as the lobes. Numerous smaller ones are located in the vascular cylinder between the larger bundles, being separated from them by narrow parenchymatous rays which are one or two cells in width. The pith consists of thin-walled parenchymatous cells with small intercellular spaces at their angles. The stelar tissue is so compact that it gives the appearance of having a continuous cambial zone; but, in the young stem, no interfascicular cambium crosses the rays, and the ray cells keep pace with the enlargement of the axis by radial elongation and periclinal divisions. Where the bundles are separated by wider rays, an interfascicular cambium may cut off connective tissue; and, occasionally, secondary xylem and phloem elements are differentiated.

The primary xylem is endarch and it usually lies in direct radial alignment with the secondary xylem vessels. (Fig. 222.) The phloem is differentiated collaterally in relation to the xylem; and consists of sieve tubes and companion cells, bounded by a pericyclic zone in which the cells become thicker walled as the stem matures. The inner cortical region is comprised of several layers of thin-walled cells, which compensate for the increasing size of the stele by tangential enlargement and radial divisions. Outside this region is an intermediate zone of smaller, more compactly organized, collenchymatous cells which may extend to the epidermis at the angles of the stem. The thin-walled cells in the outermost zone are chlorophyllose, and a number of lysigenous glands develop in this tissue close to the epidermis.

This type of gland is also found in the embryo, primary root,

leaves, floral parts, and in the pericyclic and secondary ray tissues of the stem. Stanford and Viehöver (33) have investigated them, as well as the nectaries, and state that the former are lysigenous in their development, although some of them may be formed by the enlargement of a single cell. With respect to their contents, they report that

"The glands in portions of the plant which are exposed to light are surrounded by an anthocyan-bearing envelope of flattened cells, and contain quercitin, . . . ethereal oil, resins, and perhaps tannins. The glands not normally exposed to the light are surrounded by a layer of flattened cells containing no anthocyanins; they contain gossypol."

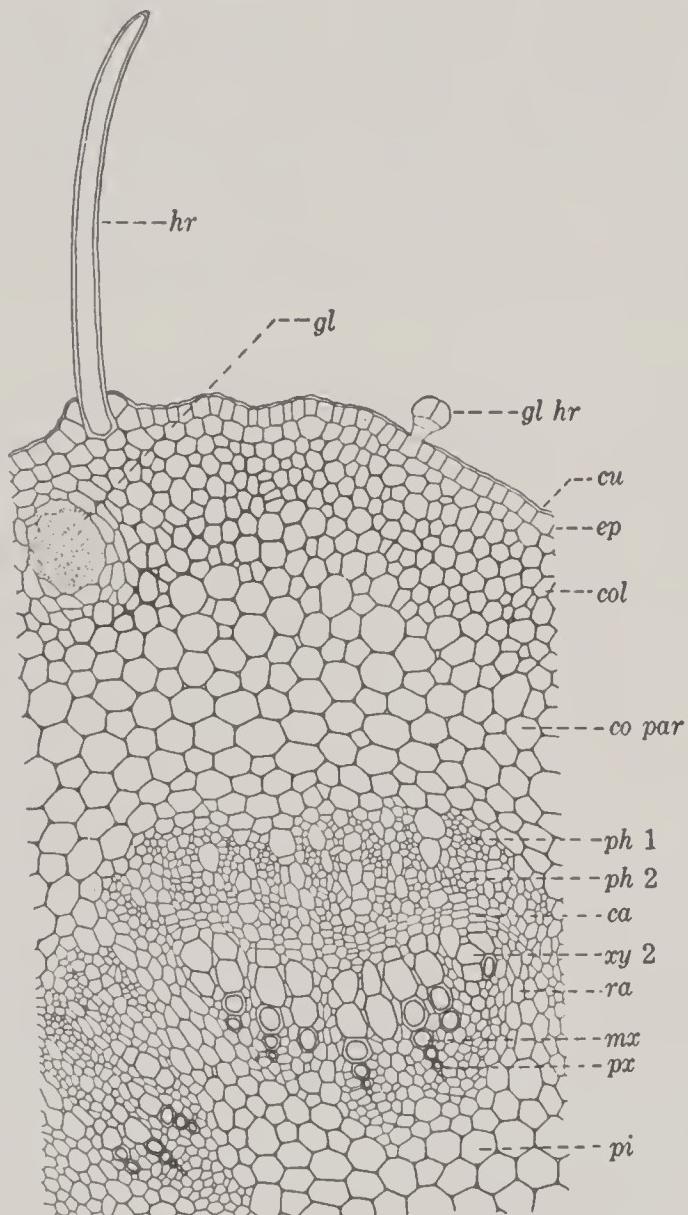


FIG. 222. Transection of portion of young stem: *ca*, cambium; *col*, collenchyma; *co par*, cortical parenchyma; *cu*, cuticle; *ep*, epidermis; *gl*, gland; *gl br*, glandular hair; *hr*, hair; *mx*, metaxylem; *ph 1*, primary phloem; *ph 2*, secondary phloem; *pi*, pith; *px*, protoxylem; *ra*, medullary ray; *xy 2*, secondary xylem.

lar and subtended by a group of basal cells, capitate, multicellular, and usually consists of a stalk of three cells, the outer, broadly wedge-shaped one bearing a terminal group of four cells that are probably glandular. As maturation of the stem proceeds, the epidermal and cortical regions become fissured,

and phellogens are produced which form a protective layer of phellem. The first phellogens are of cortical origin, while later ones are differentiated in the pericyclic parenchyma. The outer layers of the axis may become quite corky, accompanied by the development of lenticels. As secondary thickening proceeds, a large number of thick-walled fibers are produced in the secondary phloem. The secondary xylem is not heavily lignified, and the soft woody tissue disintegrates rapidly.

ONTOGENY OF THE LEAF. — The early development of the leaf and the stipules has been reported by Gore (18) as follows:

"The leaf primordium and stipule primordia arise practically simultaneously from the apical meristem of the primary axis. (Fig. 223, A, B.) The leaf primordium is rounded and collar-like at first, later tapering somewhat up to the rounded tip. As the embryonic leaf grows upward it becomes bluntly pointed. . . . There is little evidence of differentiation into petiole and blade at this stage, except the slight beginning of the plicate folding characteristic of the lamina of a young leaf. No epidermal hairs are present at this stage, although they begin their development early. The third young leaf from the tip is completely covered with them.

"The tip of this first protuberance becomes the median lobe of the palmate leaf; its base develops into the petiolar region. There soon develops on the slightly incurved margins of this primordium two pointed protuberances located about halfway between the tip and its base. These are the primordia of the two lateral lobes of the leaf. The young leaf, consisting of three lobes, now proceeds to develop in length; continued inward plicate folding, as the lobes increase laterally in size, forms a cuplike portion. (Fig. 223, B, C.) If additional lobes occur they arise in the same way and are similar in all respects. (Fig. 223, D, E.) Seven lobes is the usual number for leaves on the main axis, while on the fruiting branches of Pima and Sea Island varieties the leaves usually have three. In Mebane five-lobed leaves are commonly found on the fruiting branches. Soon the tips of the individual lobes meet and the lamina develops rapidly. The main veins appear as definite ridges on the abaxial surface of the leaf and are very thick in proportion to the rest of the leaf. The venation is palmate.

"Simultaneously with or shortly after the initial leaf primordium becomes distinct, two stipular flanking protuberances arise. (Fig. 223, B.) These are pointed and concave at first, but as they grow they widen out from the base somewhat, later become toothed, fold inward very slightly, and keep pace with the growth of the leaf. They are not folded or plicate as is the young leaf but remain more or less flattened, their interlocking hairs holding them tightly appressed to the leaves."

THE MATURE LEAF. — The leaf has an upper epidermis of brick-shaped cells with outer walls that are cutinized. (Fig. 224, A.) Stomata occur in the upper epidermis but are more numerous in the lower. Stomatal counts, per square millimeter of surface, reported by Balls (6) for the vegetative organs are: leaf, upper epidermis, 44–97, lower epidermis, 116–176; cotyledons, upper epidermis, 200,

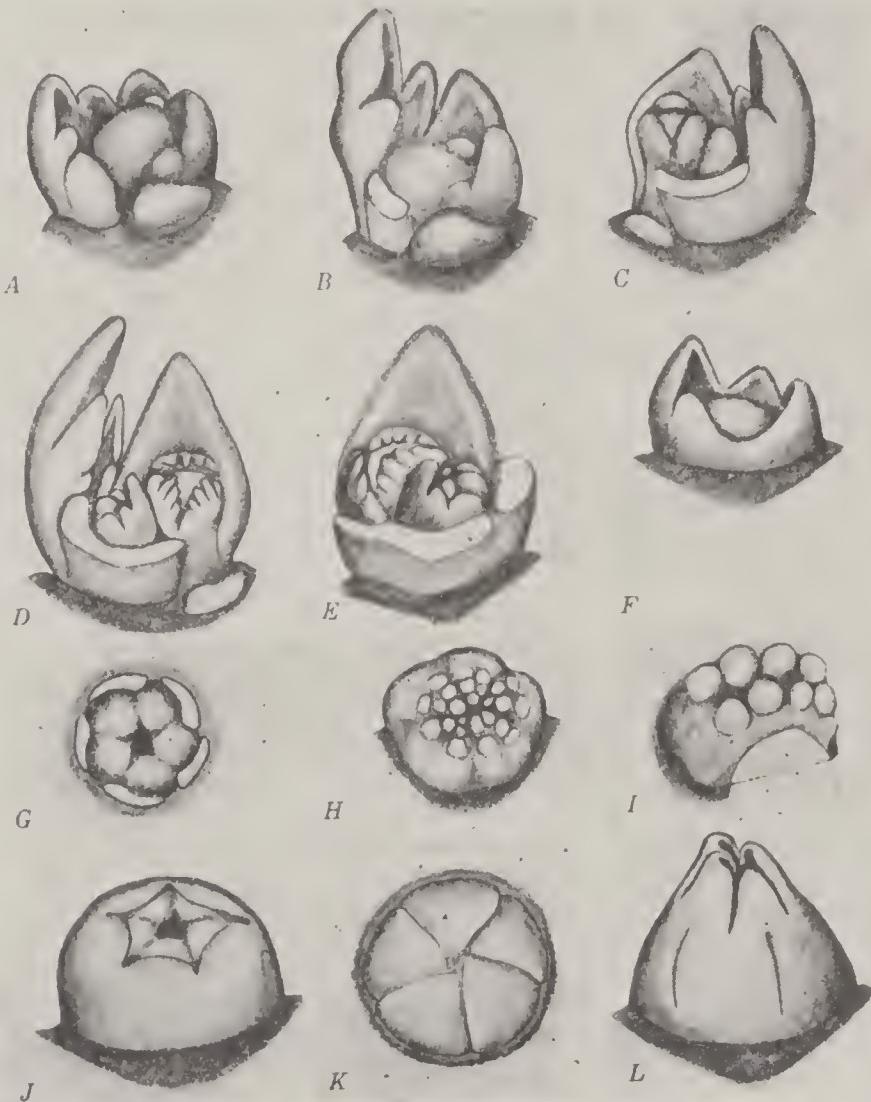


FIG. 223. *A*, growing point of cotton stem showing early stages in ontogeny of leaf, stipules, axillary bud, lobes of young leaf, and general topography of tip of main axis, drawn from above and slightly to one side, Pima; *B*, later stage in leaf ontogeny, one stipule cut away, Mebane; *C*, general topography of fruiting branch terminal, origin of bracts on floral primordium and new axillary primordium, Sea Island; *D*, later stage in ontogeny of sympodial axis showing slightly older floral bracts, Pima; *E*, later stage than figure *D*, showing origin of new fruiting branch terminal between leaf and floral primordium, Mebane; *F*, axillary bud of fruiting branch showing bractlike structure, growing point, leaf and stipule primordia of second node, Mebane; *G*, early ontogenetic stage of staminal column, petal primordia well differentiated and showing alternate staminal column lobes, Sea Island; *H*, later stage in ontogeny of staminal column showing stamen primordia in two rows on each ridge, Pima; *I*, one of five lobes of developing staminal column with stamen primordia, under greater magnification than figure *H*, Pima; *J*, young calyx with bracts removed, Mebane; *K*, developing petals, Pima; *L*, young pistil, Mebane. (After Gore.)

lower epidermis, 275; hypocotyl and stem, 20. The stoma is surrounded by two small guard cells with conspicuously thickened outer, inner, and radial walls. In the palisade region, the cells are very much elongated so that this layer comprises approximately one-third to one-half the thickness of the leaf. The underlying spongy cells are more loosely arranged with numerous intercellular spaces; and, adjacent to the enlarged midrib, lysigenous glands occur similar to those in the cortex of the stem. In some instances, these are very large and extend from the lower epidermis into the palisade layer. The lower epidermis resembles the upper except that the cells are more irregular.

The main veins have rib-like projections on the adaxial surface consisting of strands of thick-walled mechanical cells which are separated from them by several layers of thin-walled parenchyma. The vascular bundle is collateral, resembling that of the stem in the seriate arrangement of its xylem cells, in the well-defined cambium, and the rather regularly arranged groups of phloem elements. On the abaxial surface, there is a zone of compact parenchyma forming a prominent ridge beneath each of the larger veins, and this is usually reinforced by two or three layers of thick-walled cells.

Nectaries occur on the abaxial surface of the main ribs of the leaf in all cultivated varieties grown in the United States with the possible exception of *Gossypium tomentosum* Nutt. Tyler (35) reports that the number varies from one to five with one to three being most common. They appear as small, shallow, oval, pear-shaped, or sagittate pits that may be naked, although, in many varieties, there are stellate hairs protruding from the surrounding surface. Club-shaped papillae arise from the floor of the pit, each consisting of several glandular cells. (Fig. 224, A, B.) Reed (26) has described the development of the nectaries in *Gossypium hirsutum*, and reports their occurrence on the cotyledons as well as on the other foliage leaves. The papillae are epidermal in origin, and the first walls that come in are transverse so that short papillae are formed consisting of two to four cells. This is followed by a vertical division of the terminal cell, and each resulting daughter cell again divides, the new wall lying at right angles to the first cross wall. Periclinal divisions of these four terminal cells result in the formation of four central and four peripheral cells. Finally, each of the external cells divides so that a peripheral layer of eight cells is formed.

The petiole of the leaf is terete or oval in transection, and the vascular bundles are arranged in a ring with four or five large bundles and several smaller ones constituting the leaf trace. These are surrounded by thin-walled parenchyma, and there is an outer zone of small, compact cells in which glands occur similar to those found in the lamina.

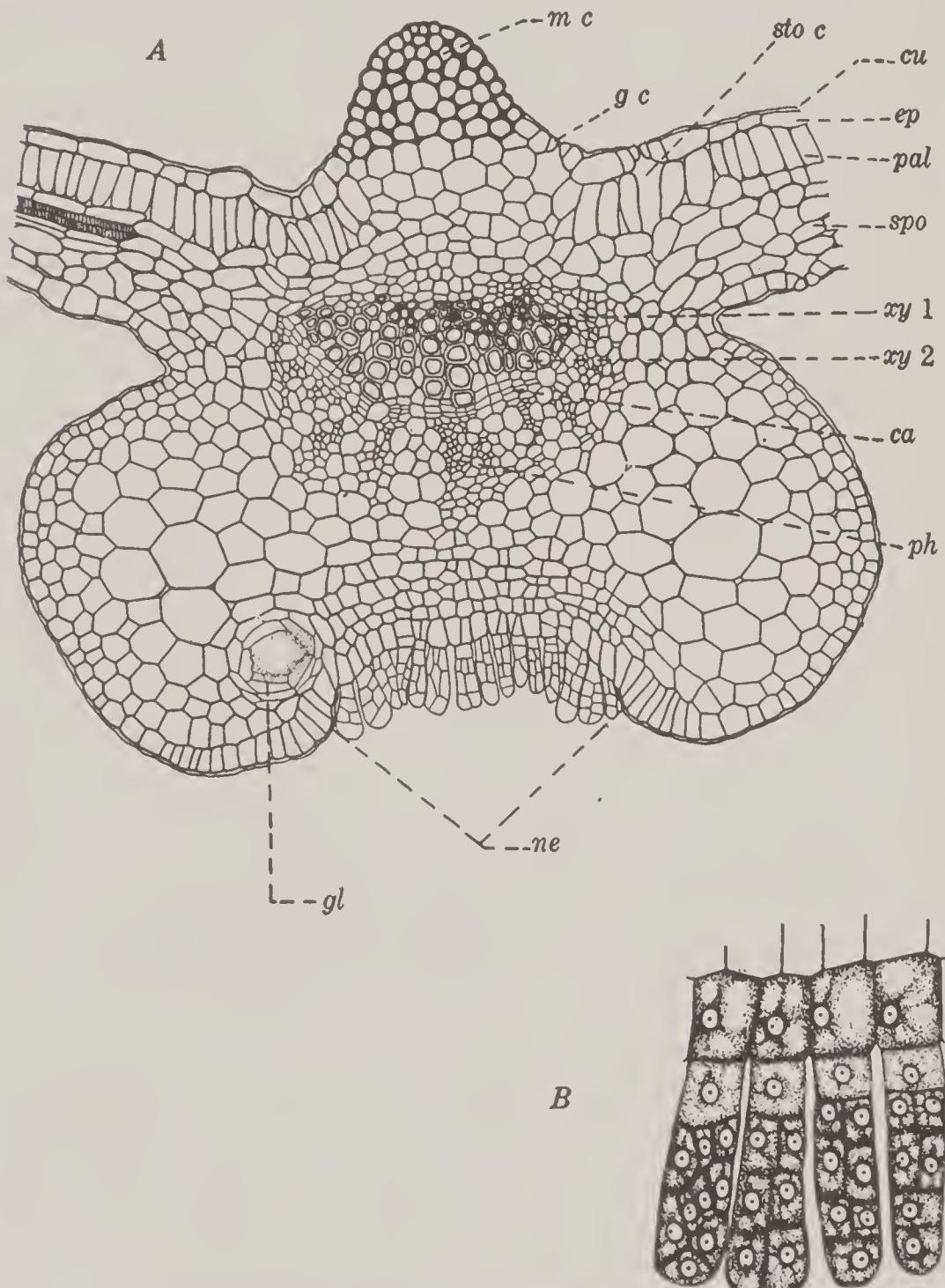


FIG. 224. A, transection of portion of mature leaf through main vein; B, detail of papillae in nectary: *ca*, cambium; *cu*, cuticle; *ep*, epidermis; *gc*, guard cell; *gl*, gland; *mc*, mechanical cells; *ne*, leaf nectary; *pal*, palisade cells; *ph*, phloem; *spo*, sponge cells; *stc*, stomatal cavity; *xy 1*, primary xylem; *xy 2*, secondary xylem.

FLORAL DEVELOPMENT. — The ontogeny of the flower has been investigated by Doak (11, 12) and Gore (18). In the development of the floral organs from the meristem of the terminal bud, the primordia of the involucre, calyx, corolla, androecium, and gynoecium arise in acropetal succession. The three bracts of the involucre appear very early in ontogeny as crescentic primordia, the first one arising opposite the leaf, and the other two following in succession. At first, the margins of the bracts are entire, but early in their development they become serrate. They increase rapidly in size; and, at maturity, form a triangular bud within which the floral organs develop until anthesis, when the unfolding petals force the bracts apart. Following anthesis and the shedding of all the flower parts, except the pistil and calyx, the bracts return to their original position so that a young fruit may have the outward appearance of a large bud.

The extra-floral nectaries of the involucre are formed comparatively late in its development. The three outer ones, which are located at the base and on the outside of the involucral bracts, occur in all American species of cotton, although they are not necessarily present in every flower. They are somewhat larger than the leaf glands, forming rounded or pear-shaped pits from the floor of which arise round secreting cells. The three inner involucral nectaries which are present in most species of cotton are located between the calyx and involucre and alternate with the outer ones. The inner nectaries are shallow and usually naked in the case of American species, but in Old World cottons may be protected by a covering of short stellate hairs.

The primordium of the calyx arises next; and, at first, forms an undulating ring of meristematic tissue. As this grows upward, five crescentic protuberances are differentiated which ultimately become the tips of the five-lobed gamosepalous calyx. The lobes of the calyx incline over the floral axis, and, for a time, enclose the primordia of the other floral parts. Further development of the calyx results in the formation of a shallow cup with a constricted throat and an undulating rim. Inequalities in the rate of growth at the apex and base of the calyx result in the dilatation of the basal portion of the tube while the throat of the calyx fits tightly over the structures within. Later, there is a reversal in the growth rate of the upper and basal regions; and, at blossoming time, the throat of the tube is greatly enlarged. The floral nec-

taries arise comparatively late in ontogeny, and consist of a ring of papillate cells which are a part of the adaxial epidermis at the base of the calyx. These are bordered by hairs that are stiff and greatly elongated.

After the divergence of the primordia of the sepals, a common stamen-petal primordium is formed from the rounded mass of meristematic tissue remaining toward the center of the axis. This first develops as a collar-like ring which grows uniformly at all points, but more rapidly at the margin, so that a saucer-like depression is formed surrounded by a thick marginal rim. Five narrow crescentic points, which ultimately differentiate into the petals, arise on this margin alternate with the sepal lobes. Each petal primordium soon develops an apical notch; and, later in development, the two halves grow at unequal rates. The longer half becomes hairy on both surfaces while the shorter one remains glabrous. It is the interlocking of the hairs of the longer halves that holds them tightly together in the convolute bud. Continued growth of the corolla results in its projection beyond the sepals, and it forms a cone-shaped structure about which the calyx is closely appressed.

While the petals are forming, the inner margin of the meristematic ring, which is the common point of origin of the petals and stamens, continues to grow upward and forms a ridge with five prominent protuberances. This structure is the forerunner of the staminal column, each protuberance producing a fascicle of stamen-primordia; and further development of the five primordial lobes results in the formation of ten paired ridges. The lobes of the staminal column are alternate with the petals, but the growth of the column and the torsion of the petals make it appear that the lobes are opposite them. Gore (18) has described the subsequent development of the staminal column:

"soon after the first spherical stamen primordia arise, other primordia appear on top and down the outside face of each lobe of the staminal column, until ten definite rows are formed. Each of these ten rows of stamen primordia, except the bottom members of each row, divides one or more times. Multiplication of stamens by division of existing primordia produces a large number of stamens, from 50 to 125 or more in the varieties studied."

As growth proceeds, the anthers become crowded and closely packed, so that their natural orientation is soon lost, and transec-

tions of the buds show the loculi cut at every possible angle. The young anthers are capitate, but finally become reniform and grooved along the line of future dehiscence. At first, there is little elongation of the filament; but just prior to blossoming, it lengthens rapidly and raises the anther several millimeters.

Doak and Gore are in general agreement with respect to the ontogeny of the pistil, which may consist of from three to five carpels. The primordial points of the carpels arise from a dome-shaped growing point surrounded by the staminal column, and these ultimately become the stylar and stigmatic portions of the pistil. At first, they grow slowly as compared with the other parts; but the upward growth of the ovary results in the projection of the young stylar structures into the staminal tube at an early age. As the undiverged bases of the carpels increase in size, internal ridges are produced which develop into the true septa of the ovary. These may be regarded as the free inturned margins of the undiverged carpels which grow centripetally and upwardly until the original cavity is divided into as many locules as there are carpels. Continued growth of the reflexed margins of each carpel forms the placentae from which the four to six ovules arise. In describing the formation of the placentae, Gore states that "from the two vertical edges of each septum the rounded placental ridges appear. The edges of these placental masses grow outward at an increasing angle toward the external carpel wall, finally becoming a flattened mass of meristematic tissue." The style and stigmas remain within the throat of the staminal cylinder until one or two days before blossoming, when an increase in the rate of growth of the style carries the stigmas beyond the staminal column and above the anthers.

THE VASCULAR ANATOMY OF THE FLOWER. — The vascular system of the floral axis is similar to that of the stem forming a dictyostele of from 20 to 30 bundles. At the involucral node, the pedicel is triangular in transection, and the two main bundles of each bract are diverged from the vascular ring at this point. They pass into the bracts at a higher level, after being further branched so that several bundles supply each bract. Slightly above this point, there is an inward divergence of an adaxial series of vascular strands which ultimately become the placental bundles. At a higher level, there is a divergence of a series of abaxial bundles which supply the outer wall of the boll, the number varying with the number of

carpels, each of which is usually supplied by ten or more bundles. The anastomosed sepal-petal-stamen group of vascular strands consists of five or more bundles supplying each sepal, three or more to each petal, and ten main bundles for the staminal column. These are successively diverged in the order named. (Fig. 225.)

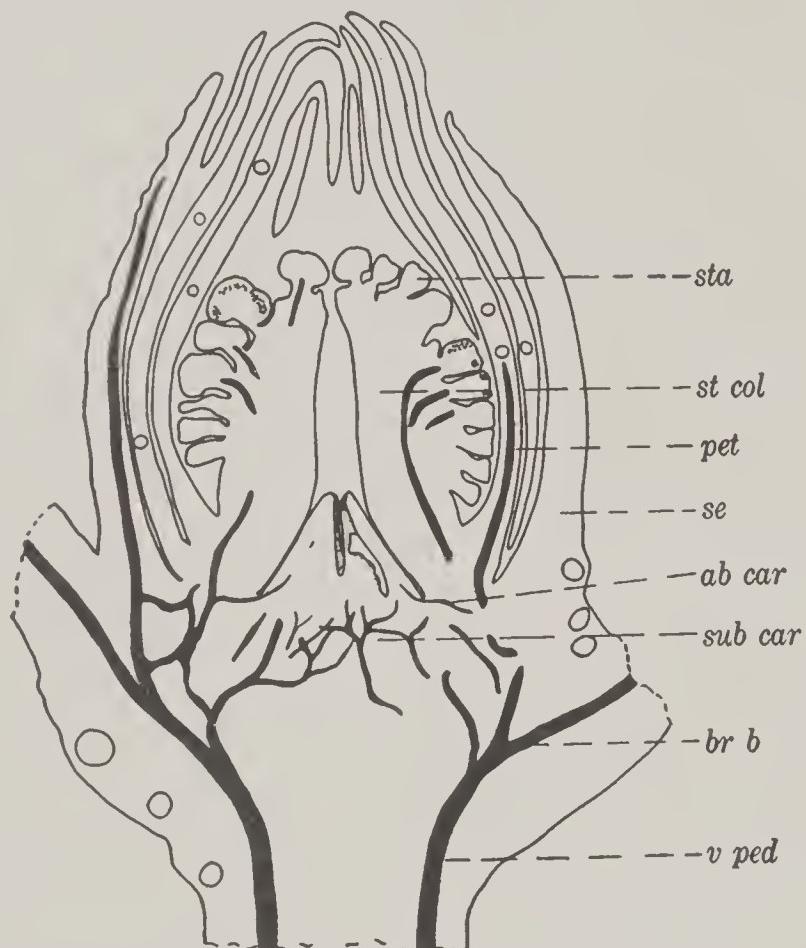


FIG. 225. Longisection of flower bud showing vascular supply to various organs. The variety is Mebane: *ab car*, abaxial carpillary bundle; *br b*, bract bundle; *pet*, petal; *se*, sepal; *sta*, stamen; *st col*, staminal column; *sub car*, subcarpillary complex; *v ped*, vascular supply to pedicel. (After Gore.)

MICROSPOROGENESIS. — Beal (8) investigated microsporogenesis in two forms of *Gossypium barbadense* L., and three Upland varieties belonging to *G. hirsutum* L. and found no observable differences in their meiotic behavior. In the development of the anthers, the outer layer of cells is differentiated as an epidermis which persists in the mature anther. The "archesporium proper arises from localized areas of the cell layer immediately inside the epidermis, the cells of which divide first by periclinal walls. The outer layer resulting from this division again divides, giving rise to two layers of tissue (vegetative) cells, while the inner layer, in due time, gives rise to the pollen mother cells." The haploid number of chromo-

somes for cultivated species of cotton is 26; but Skovsted (30, 31) has reported several species with a haploid number of 13 chromosomes, as well as a triploid hybrid in Asiatic cotton with a somatic chromosome count of 39, and tetraploids with 52.

DEVELOPMENT OF THE OVULE. — The primordia of the ovules arise on the placentae as rounded masses of meristematic cells at about the time that the locules become closed. During the development of the nucellus, a basal fold appears growing upward to form the inner integument; and as the apex of the nucellus begins to curve, a second fold initiates the outer integument, which soon overgrows the inner one. Both continue their growth until they completely cover the nucellus, except for a small micropylar opening around which the outer integument forms a lip-like ring. The inner integument is 10 to 12 layers in thickness at the time of flowering, and the outer one from six to eight layers. While the integuments develop, the ovule continues its curving growth until it becomes completely anatropous; and as the ovule assumes this position, the portion of the funiculus which is undiverged from the integument elongates greatly, forming the raphe. (Fig. 226, *B-D.*)

MEGASPOROGENESIS AND THE MEGAGAMETOPHYTE. — The early development of the archesporial cell is similar to that found in most dicotyledons. According to Gore (17),

"it has its origin from a subepidermal cell of the nucellus and arises before the differentiation of the integuments. From its division a primary parietal cell and a primary sporogenous cell are formed. . . . While this sporogenous cell increases in size and becomes the megaspore mother cell, the primary parietal cell divides many times. The other cells of the nucellus also divide periclinally and anticlinally, thus embedding the megaspore mother cell in several layers of nucellar tissue. The mature megaspore mother cell is somewhat elongated and lies quite near the chalazal end."

Reduction divisions result in the formation of a linear tetrad of megasporangia at the micropylar end of the ovule. The chalazal megaspore functions; and the outer three abort, although Balls (3) does report an anomalous condition in which the outermost or micropylar megaspore may function. In the development of the megagametophyte, three successive nuclear divisions result in an eight-nucleate stage, and it becomes an elongated narrow structure which extends close to the chalaza. (Fig. 226, *D.*) Just prior to

fertilization, there are three antipodal nuclei at the chalazal end of the gametophyte, two centrally located polar nuclei, and the megagamete with two synergids at the micropylar end. At this time, the megagametophyte is surrounded by nucellar tissue which is 20 to 25 layers in thickness except at the chalaza. The antipodal nuclei are ephemeral and disappear by the time the flower opens.

FERTILIZATION. — Various estimates have been made as to the length of time required between pollination and fertilization. These range from approximately 15 to 36 or 40 hours. The insect-borne pollen grains reach the stigmatic surface of the pistil which is covered with unicellular hairs, and the pollen tubes rapidly penetrate the tissue of the stigma and style. Once inside the ovary, the pollen tube follows the placenta, growing within the tissue or on the surface; and, upon reaching the base of an ovule, travels up the funiculus toward the micropyle. The path of the pollen tube through the micropyle and into the

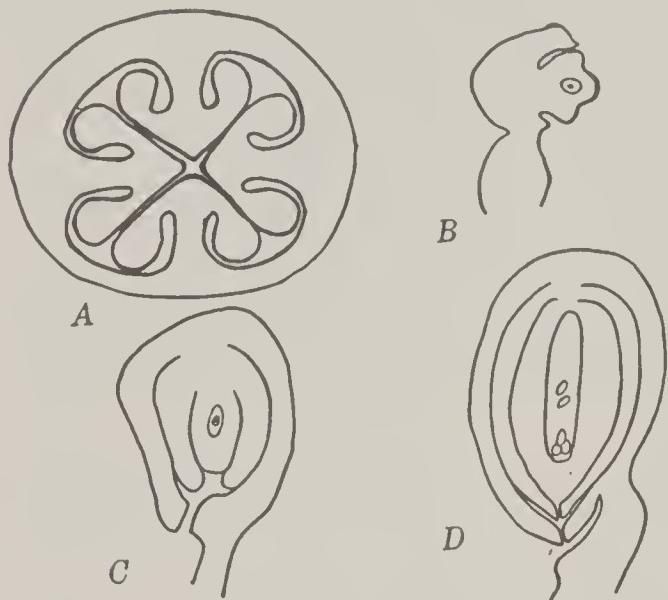


FIG. 226. *A*, diagram of transection of young four-locked ovary showing placentae and development of young ovules; *B*, *C*, and *D*, successive stages in development of ovule. (*B* and *C*, after Gore.)

nucellar tissue is variable, the tendency being for the tube to penetrate for a distance between the integuments, or between the inner integument and the nucellus, before entering the latter. This results in the tube having a more or less branched or haustorial appearance.

Following the penetration of the gametophyte by the pollen tube, double fertilization is effected. One microgamete fuses with the megagamete to form the zygote, while the second microgamete undergoes a triple fusion with the polar nuclei to form the primary endosperm nucleus. Variation in the details of the triple fusion has been reported, but most frequently the polar nuclei fuse before the union with the second microgamete. In other instances, the fusion of the two polar nuclei and the second microgamete seems

to be simultaneous. After the formation of the endosperm nucleus, free nuclear divisions occur until there may be from twenty to twenty-five endosperm nuclei in the embryo sac. Wall formation is initiated at the micropylar end of the embryo sac, and finally a massive endosperm is produced, which is later resorbed by the embryo until only one layer remains.

EMBRYOGENY. — The development of the cotton embryo has been described by Reeves and Beasley (28). The first division of the zygote, which usually occurs the second day after fertilization, is transverse; and this is followed by a vertical division of the apical cell and occasionally of the basal cell. A short suspensor is formed, but it apparently disintegrates early in ontogeny; and Balls' (3) statement that there is no suspensor may be explained by this fact. The two apical cells divide to form a quadrant, and from this the eight-celled embryo arises about the fourth day. Divisions of each of the eight cells result in a sixteen-celled embryo that is usually five-tiered.

The initial stages occur before there is any appreciable increase in the size of the embryo; and in about nine days, the cotyledons and hypocotyl are differentiated. This is followed by a period of rapid growth so that in twelve to fifteen days provascular strands develop, and the palisade cells differentiate in the cotyledons. At about this time, the resin glands appear, being formed lysigenously from two or three cells. By the eighteenth day or before, oil, starch, pentosans, gossypol and proteins are present in the embryo. During the closing periods of growth, the embryo continues to increase in weight until about the thirty-fifth day, when it begins to lose weight by desiccation, reaching an approximate equilibrium by the forty-third to forty-seventh day.

DEVELOPMENT OF THE FIBER. — The development of the fiber has been described by Balls (5), Hawkins and Serviss (21), Gulati (19), Singh (29), and Farr (14, 15, 16); and, recently, its structure has been investigated by Kerr (22), Anderson and Moore (2), and Anderson and Kerr (1).

The ontogeny of the fiber may be divided into two phases, the first dealing with its initiation and elongation; and the second with the thickening of its wall. The epidermal cells nearest the chalazal end of the ovule are the first to develop and produce the longest fibers, while those at the micropylar end arise later or may fail to develop at all. On the day of flowering, the individual

epidermal cells that are to become fibers begin to swell slightly; and at the end of twelve hours, they have a bulbous appearance and the cells are more vacuolate. (Fig. 227, A.) After twenty-four hours, the tubular fiber cells are much elongated and have usually attained their full diameter. (Fig. 227, B.) By the second day, there is a differentiation of the fibers so that some are longer with pointed tips, while others are short and rounded. At the end of three days, they appear definitely tapered for approximately a quarter of their total length. At this time, the cells have large



FIG. 227. A, transection of epidermis of ovule on day of flowering showing origin of cotton hairs; B, same, 24 hours after opening showing elongation of hairs. The variety is Mexican Big Boll. (Photomicrographs by Lang.)

vacuoles and the walls are still thin, since during the entire period of elongation the protoplast of the hair is enclosed only by a primary wall containing pectic substances, cellulose and probably waxes. Anderson and Kerr state that there is no evidence of cutin at this time, but that there is "a coherent skeleton of cellulose from the first day of its appearance." This is in contrast to reports by other investigators [Farr and Eckerson; Hess, Trogus and Wergin; Sakostschikoff, Korsheniovsky, and Rutikoly — reviewed in Anderson and Kerr (1)] that cellulose does not appear in the walls until from five to as many as thirty-six days after flowering. This difference may be accounted for on the basis of the small amount of cellulose present, and its effective insulation by pectic substances.

At this stage, the lint can be differentiated from the fuzz by the relative size of the two types of epidermal outgrowths. The development of fibers from the epidermal cells may continue for several days after flowering, and Anderson and Kerr suggest that those produced during the first two or three days become the lint while the hairs that are formed later become the fuzz. Brown (9) attributes the differentiation of some of the epidermal cells into lint and others into fuzz, to hereditary characters; pointing out that, regardless of cultural conditions, certain varieties always have a low percentage of lint in comparison with the amount of fuzz, while others have a relatively high percentage of long hairs. While the two types of hair initials are at first similar in structure, they become very unlike at maturity. The lint may vary in length from $\frac{5}{8}$ to 2 inches, while the fuzz remains very short.

In connection with the origin of the later formed fibers, Farr (16) has shown that they do not all arise from the original epidermal cells, but from daughter cells which have been derived from the former by cell divisions that occur subsequent to flowering. There is a thirty-two-fold increase in the surface area of the ovule during the first twenty days of its development, and only a two-fold increase in the surface dimensions of the epidermal cells. The increasing surface area cannot be accounted for entirely on the basis of cell enlargement, and continued cell divisions of epidermal cells must occur, to compensate for the growth of the maturing ovule. This fact is in harmony with the recent findings relative to continued fiber formation.

The nutrition of the developing fiber was attributed by Barratt (7) to liquid in the intercellular spaces of the boll cavity, but Farr (14) regarded this as unlikely and failed to find any evidence of "a liquid or semi-liquid substance in the boll cavity." It seems probable that nutrition during the development and maturation of the fiber takes place only through its basal connection with the adjacent tissues of the integument.

The lint usually attains its full length by the end of the fifteenth to twenty-fifth day of growth, the period of elongation apparently depending upon several factors, including environmental conditions, the time of the year that the flower opens, as well as the variety. Following this, the second phase of fiber development begins involving secondary wall thickening. Earlier investigations by Balls (5) have been confirmed by Kerr (22) with respect

to the periodic deposition of the lamellated secondary wall. In this connection, Balls stated that

"the secondary thickening of the wall proceeds intermittently under normal Egyptian field crop conditions, being arrested each afternoon; that the cellulose of the hair consequently consists of a number of concentric shells, layers, or 'growth-rings,' each one representing one day's growth, with the exception of that of the primary wall; and that the so-called fuzz-hairs are analogous with the lint-hairs, though their growth-rings are coarser and more sharply demarcated."

In describing the structure of the walls he found that the

"hairs are covered, outside the cellulose of the primary wall, by a cuticle, bearing wax, which is structurally . . . identical with the cuticle of the testa, while it is structurally and chemically distinct from the cellulose. The secondary wall, but not the primary, is traversed obliquely to the hair axis by simple pits which are rarely visible except in the living hair, and to these pits is due the twisting of the hair and its characteristic convolutions after death."

The death of the cell occurs following the opening of the boll, with the resultant loss of water which causes the fiber cells to collapse, forming flattened tubes with many twists.

Kerr found that during the period of secondary wall formation there are two lamellae laid down each twenty-four hours which together constitute a daily growth ring. These two zones differ in their porosity, the compact zones being deposited during the day and the porous ones at night. The differences in porosity, which result in the lamellated appearance of swollen fibers, are correlated with temperature fluctuations, and the contrast between adjacent porous and compact lamellae is greater when the night temperature falls below 20° C., while there is less differentiation between the zones when it does not fall below 22° C. Thus, while Kerr confirmed Balls' observations regarding the diurnal deposition of the growth rings, they are not in agreement with respect to the method by which this is accomplished. Balls suggested that the ring was formed in the night and early morning, and that growth stopped entirely during the hot afternoons; while Kerr attributes the rings to the formation of a continuous matrix of cellulose laid down in different densities.

Anderson and Moore (2) investigated the effect of continuous light on the structure of the walls of fibers and collenchyma and found that the reaction of the two tissues to this factor is quite

different. In fibers grown under continuous artificial light there are no lamellations, such as appear in fibers grown under field conditions and then swollen in cuprammonia and subjected to pressure. (Fig. 3.) On the other hand, continuous illumination has no effect upon the conspicuous lamellations of the collenchymatous cells. Although the light effect may be correlated with the temperature relations determined by Kerr, it is suggested that light may have an effect independent of temperature. The fibers grown under continuous illumination have the same convolutions and reversals as those grown in the field, and the spirally wound strands of cellulose exhibit the same structural pattern. Limited tests also indicate that the tensile strength of the unlamellated fibers grown under continuous illumination is not significantly different from that of lamellated ones grown in the field.

The structure of the fiber has been represented diagrammatically by Anderson and Kerr (1); and they have described it as follows: (Fig. 228.)

"1. A primary wall containing cellulose and pectic substances. The cellulose micelles in this wall are grouped into delicate anastomosing threads which have at least two systems of orientation: (a) a flat right-hand spiral, (b) a flat left-hand spiral, and probably also (c) a transverse position. All three systems seem uniform over the entire surface of the fiber cell.

"2. A secondary wall composed of many lamellae of cellulose. The lamellae are not separated from one another by non-cellulosic substances but represent dense and less dense areas of cellulose. The layers are formed of systems of spirally wound branching threads, and the direction of the spiral is reversed at frequent intervals.



FIG. 228. Diagram of mature cotton fiber. The apparently structureless primary wall of cellulose and pectic substances is shown at base. The next layer represents the cellulose structure of primary wall with its three systems of cellulose threads. Zone 3 shows first layer of secondary wall at point of a reversal. Zones 4 and 5 represent second and third layers of secondary wall. The growth rings formed by the alternation of zones of dense with zones of less dense cellulose are shown at top of figure. (After Anderson and Kerr, *Ind. and Eng. Chem.*)

"3. Frequently the pattern of spirals first appearing in the secondary wall is not similar to that in subsequent layers of the wall. Most of the layers of the wall, however, follow a pattern that is established soon after secondary thickening has begun."

The strength of a fiber is dependent primarily upon the thickness of the cell wall, and not necessarily upon the diameter of the cell since some large fibers may have relatively thin walls. Strength and length are greatly affected by variations in the environmental factors, as well as by the genetic constitution of the strain of cotton grown. Fineness in quality is conditioned upon the diameter of the fibers together with the thickness of their walls; and the silky texture of Sea Island cotton is related in part to the fact that it has fibers of a somewhat smaller caliber than a variety such as the Indian wool cotton. Color and luster may be associated to some extent with cultivation and selection, the majority of wild cottons being brownish in shade, while the cultivated varieties tend to be white, cream-colored, or less frequently brown. The luster of the lint seems to be associated with the reflection of light from the cutinized surface of the hair; but according to Balls (4), it also results from the translucence of the fibers and the refraction of a certain proportion of the light in addition to its reflection from the concave surfaces within the fiber.

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CHAPTER XV

UMBELLIFERAE

APIUM GRAVEOLENS

THE parsley family is a large one consisting chiefly of herbaceous plants which may be annuals, biennials, or perennials. Among the more important economic representatives are celery,



FIG. 229. Habit of celery plant at time of harvest. (Photograph by J. Horace McFarland Co.)

Apium graveolens L.; parsnip, *Pastinaca sativa* L.; carrot, *Daucus carota* L.; and parsley, *Petroselinum hortense* Hoffm. The family name is derived from the character of the inflorescence, which is

usually a compound umbel with secondary divisions known as umbelllets. The fruit is also characteristic and is called a schizocarp. It is composed of two dry carpels or mericarps which cohere



FIG. 230. Mature plant at time of flowering showing floral axes and umbels. (Courtesy of Ferry-Morse Seed Co.)

by their inner faces during maturation, but separate when ripe, each being suspended from its summit by a branch of the slender forked carpophore.

Celery is an important salad crop and is grown throughout the United States, especially in New York, Michigan, Oregon, Califor-

nia, and Florida. The several varieties are classed as self-blanching, and green or winter types; and in the former group, Golden Self-Blanching represents about one-half of the total crop according to Jones and Rosa (11). A form known as celeriac, *A. graveolens*, var. *rapaceum*, D. C., is grown to a limited extent. In this type, 2 to 4 inches of the fleshy root is edible.

The celery plant, like the parsnip, is normally a biennial, although under certain conditions it develops as an annual. In the course of the usual biennial cycle, a well-developed root system, a short crown stem, and a rosette of leaves are produced the first year. (Fig. 229.) The second year, the much branched stems or seed stalks elongate, producing a shrubby plant 2 to 3 feet in height. (Fig. 230.) These bear compound umbels of small white flowers which produce flattened fruits toward the end of the second season.

A common practice in growing celery is to plant the seed in beds from which the seedlings are transplanted three to four months later; and, at the end of the first season, the crop is ready for marketing. Occasionally, premature seeding occurs and the plant develops flowers and fruits during the first season. There is considerable variation in this regard, and in general, the vigorously growing early varieties are most likely to go to seed the first season. Thompson (25) has pointed out that "the environment seems to control the expression of the hereditary factor or factors for annual flowering and for seed." The environmental factors which may inhibit seed stalk development are those which involve any serious check in growth. These include freezing, stunting of plants by overcrowding in the transplanting flats, and water deficiency. High temperature, 70° F. or above, tends to prevent premature seeding unless the seed stalks have already started prior to being subjected to this temperature. On the other hand, plants subjected to relatively low temperatures, 40° to 50° F., for two weeks or longer are likely to seed prematurely, and this may occur when plants are hardened in a cold frame in early spring.

GENERAL MORPHOLOGY

THE ROOT. — The primary root system, consisting of a tap root and its laterals, becomes very well developed in regions where the plants are grown from seed sown in the open ground. When transplanting is practiced, the tap root is destroyed and the fibrous system is comprised of a large number of adventitious roots that

grow out from the base of the plant. Thompson (24) states that the major portion of the roots occupies the upper 6 inches of soil, many of them being within 2 or 3 inches of the surface while a few penetrate to a depth of 2 feet or more.

THE SHOOT. — The subconical, fleshy stem remains short during the first year and bears a spiral rosette of leaves.

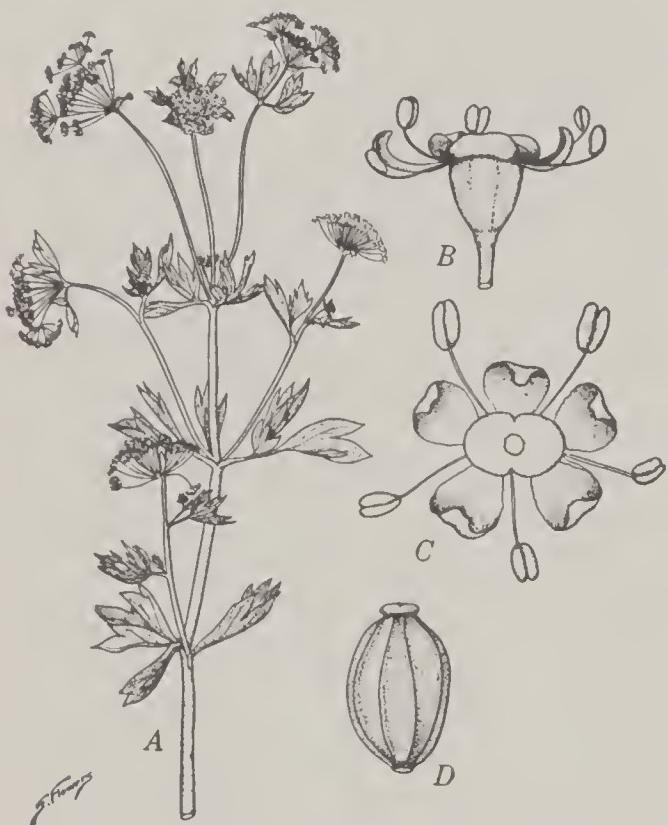


FIG. 231. A, habit of inflorescence; B, lateral view of flower; C, face view of same; D, fruit.

one. The blade is odd-pinnately compound, and usually there are two or three pairs of stalked leaflets. These are pinnately lobed or compounded, and the ultimate divisions are broadly wedge-shaped with coarsely dentate or crenate margins.

THE INFLORESCENCE AND FLOWER. — The flowers are borne in compound umbels which may or may not be subtended by an involucre, and involucels may or may not subtend the umbelllets. The flowers are perfect and epigynous, with calyx lobes that are rudimentary or lacking. The small white or greenish-white petals are incurved at their tips. Alternate with them are five stamens with very slender filaments and versatile anthers which are diverged at a level above the top of the ovary. The pistil consists of two carpels which cohere during early development to form a two-loculed ovary terminated by two distinct styles. (Fig. 231.) The

bases of their petioles overlap one another and these, with a variable portion of the fleshy stem, constitute the edible portion of the plant. The number of leaves is not constant, but commonly there are 20 to 25 in the rosette, including the small, immature, centrally located ones. The outer 12 or 15 leaves are large, with somewhat erect petioles that range from 4 to 10 inches in length. The petiole is glabrous, crescentic in transection with a prominently ribbed abaxial surface, and a relatively smooth concave adaxial

stylopodium, which is characteristic of the pistils of most umbellifers, is inconspicuous in celery. In each locule, a single seed is produced, and the schizocarp separates at maturity to produce two one-seeded mericarps.

ANATOMY

THE FRUIT AND SEED. — The schizocarp is flattened laterally and the mericarps are pentagonal in transection. (Fig. 232, A, B.) Winton (32) and Kondo (13) have investigated the histology of the

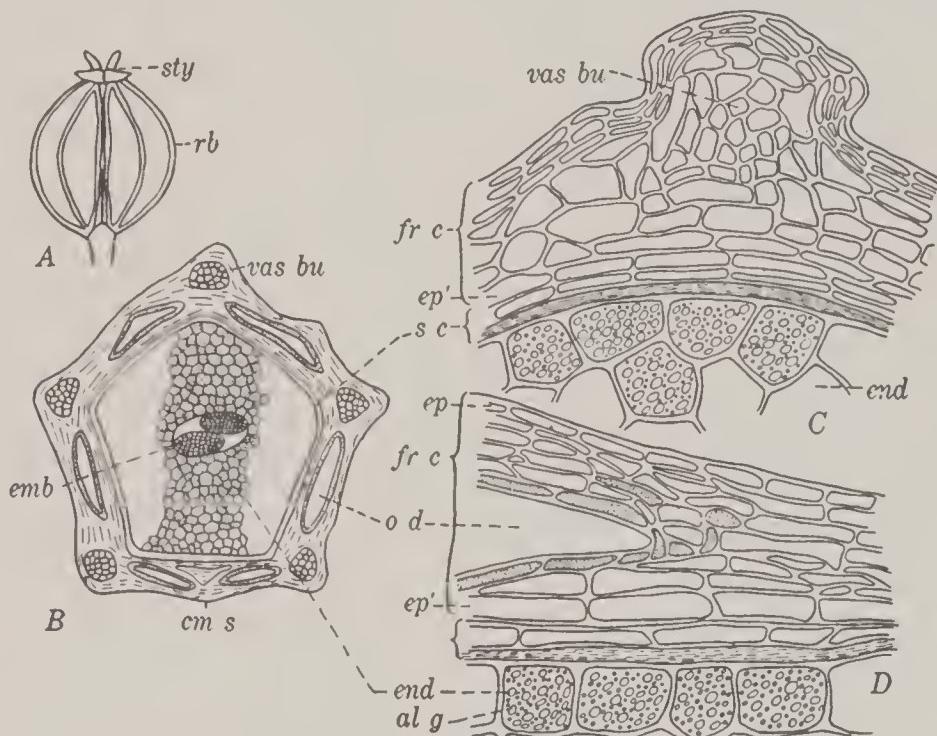


FIG. 232. A, diagrammatic side view of schizocarp; B, transection of mericarp; C, section of fruit and seed coat through rib; D, transection of fruit and seed coat through oil duct: al g, aleurone granules; cm s, commissural surface; emb, embryo; end, endosperm; ep, outer epidermis of fruit coat; ep', inner epidermis of fruit coat; fr c, fruit coat; od, oil duct; rb, rib; sc, seed coat; sty, style; vas bu, vascular bundle. (Redrawn and adapted from Kondo, Ohara Institute.)

fruit, which conforms in its general characters to the umbelliferous type. The fruits are minute, somewhat broader than long, and the mericarps have five rather pronounced primary corky ribs, each of which is traversed by a fibrovascular bundle. In the intervals between the ribs are one to three oil ducts, and there are two on the commissural side of the mericarp. Kondo reports that he found one oil duct in each interval in seven of the varieties investigated, and in only two European types were two to three present in each furrow. The pericarp, which consists of from seven to ten rows of parenchymatous cells, is marked with delicate striations and papil-

iae that are more or less evident in the form of warty protuberances. The cells of the epicarp or outer epidermis are small and isodiametric, and in surface view, are sinuous in outline. The oil ducts in the mesocarp are surrounded by a layer of polygonal cells which become brownish at maturity, and the bundles located in the ribs are accompanied by groups of sclerenchymatous cells. The somewhat elongated cells of the inner layer of the mesocarp are broader than those of the endocarp. Winton states that they are usually transversely oriented, but that it is not uncommon for them to be arranged with their long axes in other directions. The endocarp or inner epidermis is composed of narrower cross cells, which are transversely elongated or occasionally develop in a parqueted or mosaic arrangement.

The mature mericarps, each the product of the development of one of the carpels, separate along the commissural line and are suspended from a branched carpophore. This is a unique structure peculiar to the fruit of the Umbelliferae and has been interpreted by some investigators as being axial — that is, as a prolongation of the receptacle between the carpels. Others regard it as being appendicular and derived from portions of the two carpels. Jackson (9) has studied the structure on the basis of its development in the flower and fruit and has concluded that

"a small basal portion is usually receptacular or axial; by far the greater part is appendicular. . . . It represents an innermost, ventral portion of the two carpels and consists chiefly of the ventral traces of these carpels. Associated with the traces in the formation of this structure is a greater or lesser amount of adjacent non-vascular tissue."

In the mature fruit, the point of separation of the mericarps from the carpophore begins at the level at which the stele of the receptacle branches to form the peripheral and central bundles. The peripheral bundles constitute the vascular supply for the two mericarps, while the two central bundles form the carpophore. This consists of the two bundles, the large lignified parenchymatous cells which lie between them, and some non-lignified parenchyma which dies as the carpophore and fruit mature. The break which separates the carpophore into two branches occurs in the lignified parenchyma between the central bundles so that each carpophore-half consists of one central bundle.

The seed has a thin coat consisting of an outer layer of large cells and an inner zone of several rows of crushed cells. The cells

of the abundant endosperm, which completely surrounds the small embryo, are thick-walled and contain fat and aleurone grains. (Fig. 232, D.) No starch is present and Kondo reports the absence of crystals of calcium oxalate which are frequently found in the endosperm of some umbelliferous seeds. The embryo is straight and lies in the endosperm with the tip of the minute primary root inclined upward.

DEVELOPMENT OF THE SEEDLING. — The germination and growth of the seedling are relatively slow. In commercial practice, the seed is either sown in outdoor seed beds, which is the custom in the

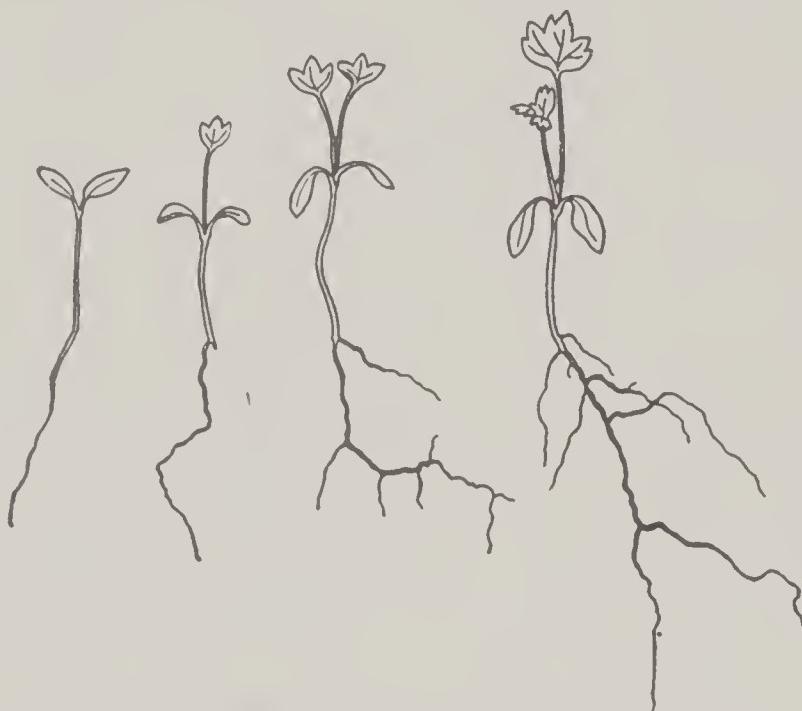


FIG. 233. Stages in development of celery seedling.

South; or grown in hotbeds or cold frames, as is the common method in the North.

The primary tap root develops laterals which are arranged in two double rows; and, following the emergence of the narrowly ovate cotyledons, the first two foliage leaves expand. The petioles are slender, and the simple, three-lobed blades have serrate to dentate margins. (Fig. 233.) When the crown of the plant has reached a diameter of $\frac{1}{2}$ to $\frac{3}{4}$ of an inch, it is transplanted.

ANATOMY OF THE ROOT. — The slender primary root has a diarch protostele, and resembles the primary root of parsnip, as described by Warning (28), in the principal details of its structure. Its ontogeny follows Janczewski's (10) third type in which there is a definite plerome and periblem, and a combined calyptrogen-dermat-

ogen layer. The plerome produces the stele; the periblem, the cortical tissues; and the calyptrogen-dermatogen layer, the root cap and epidermis.

The cortex of the young root consists of several layers of parenchymatous cells limited outwardly by the epidermis which produces a large number of root hairs. The endodermis is not defined very early in ontogeny by the development of Casparyan strips, but its position may be readily determined with reference to the pericycle which lies immediately centrad to it. The pericyclic cells become enlarged and some of them undergo a series of oblique

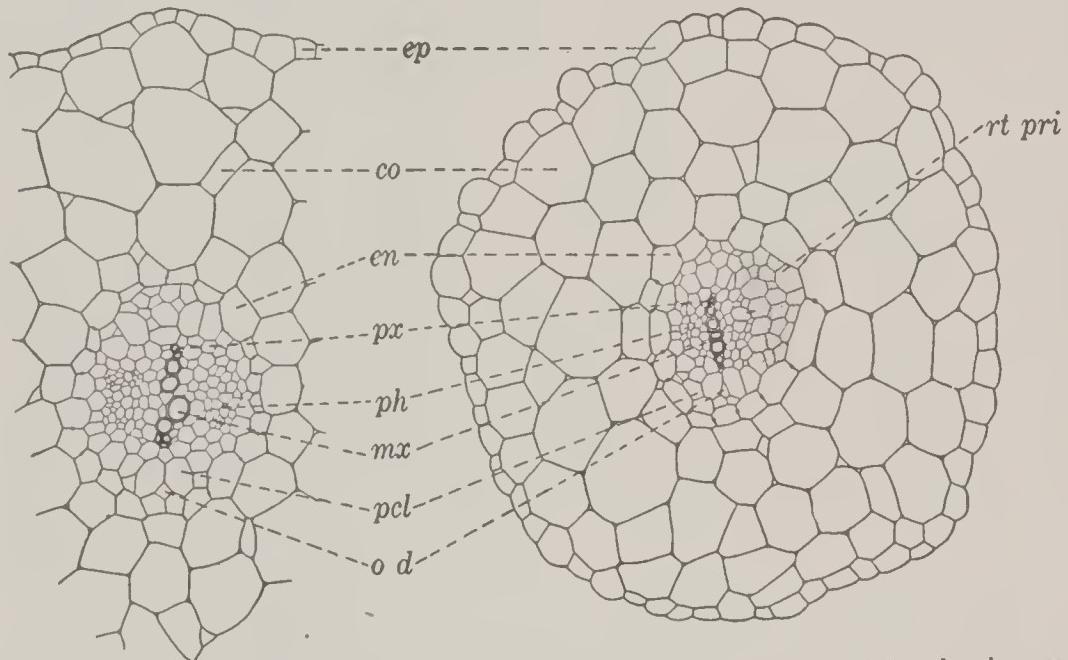


FIG. 234. Left, transection of young primary root showing stele; right, development of lateral root from pericyclic tissue: *co*, cortex; *en*, endodermis; *ep*, epidermis; *mx*, metaxylem; *od*, oil duct; *pcl*, pericycle; *ph*, phloem; *px*, protoxylem; *rt pri*, root primordium.

longitudinal divisions which result in the formation of the characteristic primary oil ducts found in this family. These lie in two arcs, each of which contains about nine ducts. The central one, which lies directly outside the protoxylem point, is quadrangular in transection while those lateral to it are usually triangular. (Fig. 234.)

Trécul (27) and van Tieghem (26) have described the development of these ducts in detail, and de Bary (3) has summarized their work. The first two oil ducts to be cut off in the pericycle are quadrangular in transection and located 180° apart. The two protoxylem points of the diarch xylem plate which later differentiate in the plerome lie immediately centrad to them. The formation of the two centrally located primary oil ducts is schizogenous,

and is initiated by the radial elongation of two adjacent rectangular pericyclic cells. Then an oblique wall comes in at about a 45° angle to the radial wall between the two pericyclic cells involved in the formation of the duct. (Fig. 11, A.) This results in the cutting of each pericyclic cell into two daughter cells, one of which is large and five- or six-angled, the other small and quadrangular in transection. The two quadrangular cells lie at the outer limit of the pericycle while the five-angled ones extend through the entire width of the pericycle. These four cells have a common angle at a midpoint on the radial wall between the original pericyclic cells, and the oil passage is formed by a splitting of the walls along their middle lamellae beginning at this point. This results in a quadrangular passage which is limited externally by two small pentagonal cells and internally by two hexagonal ones. (Fig. 11, B.)

At the time that the pericyclic ducts are being formed, the primary phloem is differentiating; and its position can be determined early in ontogeny by the formation of a primary duct in each phloem group adjacent to the pericycle. These appear to be formed schizogenously in a manner similar to the pericyclic oil ducts except that they are bounded externally by two pericyclic cells and internally by three or more phloem cells so that they are pentagonal in transection. (Fig. 11, C.) Before the metaphloem is completely differentiated, the protoxylem begins to mature. This proceeds centripetally from two points centrad to the central pericyclic ducts and continues until a solid diarch xylem strand is formed. The strand is narrow and from five to ten cells from one pole to the other. The protoxylem elements are annular and spiral, while the wall thickenings of the metaxylem are spiral-reticulate and reticulate. The primary xylem and phloem are separated by a zone of interstitial parenchyma.

LATERAL ROOTS. — The first lateral roots arise from the pericycle at approximately the time that the maturation of the primary xylem has been completed. The root primordia do not form directly outside the protoxylem points, as is frequently the case in lateral root formation; but, instead, are developed in arcs of the pericycle to the right and left of the diarch xylem strand. (Fig. 234.) This may be related to the fact that the arcs of pericyclic cells abutting the protoxylem points are involved in the formation of the primary oil ducts. The origin of the lateral roots at these

loci results in their alignment in four longitudinal rows which tend to be paired, although the torsion of the root may make the orientation appear to be spiral.

The ontogeny of the lateral roots is similar to that of the primary root, and its histogens follow the same developmental sequence as in the main axis. As the growing point is formed by tangential and radial divisions of the pericyclic cells, the endodermis is forced outward; and the emergence of the lateral root through the cortical and epidermal tissue is accomplished by a rupturing and resorption of the cells.

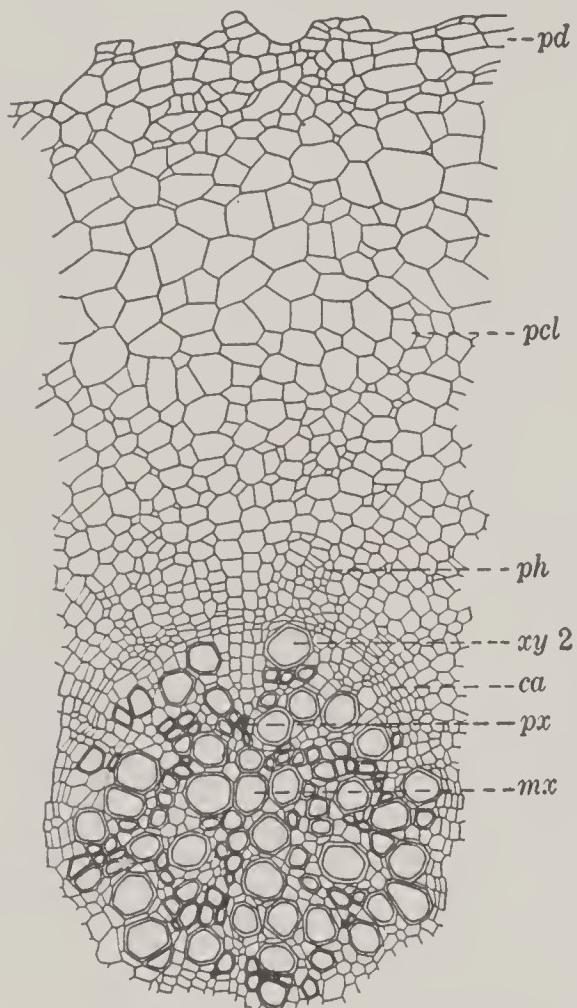


FIG. 235. Transection of sector of old root showing secondary thickening: *ca*, cambium; *mx*, metaxylem; *pcl*, pericyclic parenchyma; *pd*, periderm; *ph*, phloem; *px*, protoxylem; *xy 2*, secondary xylem.

SECONDARY THICKENING OF THE PRIMARY ROOT. — The first cambial activity occurs in the interstitial parenchyma immediately centrad to the phloem. There is a progressive lateral activation toward the primary xylem poles which may involve the pericyclic cells over those points. In most instances, the cells produced by the active tissue outside the protoxylem points are parenchymatous so that two well-defined rays are formed.

The secondary xylem vessels are laid down in radial rows, one to two or three cells in width. (Fig. 235.) This approximate

radial alignment may be maintained, except that there is also some radial and tangential separation of the vessels owing to the activity of the adjacent parenchymatous cells. The vessels are large with loosely reticulate or reticulate-pitted walls. The end walls of the vessel segments are commonly transverse and the segments are two to five times as long as broad. The cells of the secondary xylem parenchyma are thin-walled, isodiametric in transection, and approximately the length of the vessel segments.

There is an extensive development of secondary phloem which forms a broad zone consisting of groups of sieve tubes, companion cells and fibers, separated by rays of parenchyma. Numerous oil ducts occur in the phloem region which resemble the primary ones except that the number of epithelial cells is ordinarily greater.

The rapid development of secondary stelar tissue results in an early disorganization and rupturing of the cortical and epidermal regions. The endodermis is broken; and, as disintegration proceeds, the pericyclic cells divide both anticlinally and periclinally so that a zone of parenchymatous tissue is formed. The peripheral portion becomes a periderm, and the phellem is several cells in thickness, being renewed by a phellogen that also cuts off some phelloginal cells on its inner face.

VASCULAR TRANSITION. — The transition from the radial exarch arrangement of the stele of the root to the collateral endarch orientation of the vascular tissues in the cotyledons takes place in the upper hypocotyl. The change is abrupt, being accomplished within the space of a few millimeters. The first stage consists of the segmentation of each of the primary phloem groups into two separate groups. At the level at which this segmentation occurs, there is a reorientation of the centrally located metaxylem elements which, instead of forming a continuous spindle-shaped zone from one protoxylem pole to the other, differentiate laterally so that parenchymatous cells occupy the center of the stele.

At higher levels, there is further lateral differentiation of the metaxylem. The polar sectors of protoxylem are oriented in such a way that the later-formed metaxylem cells are tangentially placed and separated from the former by parenchymatous cells. The phloem groups, each of which has an oil duct, lie in an approximately collateral position with respect to the protoxylem, and lateral branches occupy a similar relation to the primary xylem that with them forms the lateral traces of each cotyledon. The vascular supply to each cotyledon consists of three bundles. The large median bundle, sometimes called a "double bundle" or "triad," is comprised of a protoxylem strand, a portion of the metaxylem lying tangential to it, and two groups of phloem which are collateral with the metaxylem. The two smaller lateral bundles are collateral.

At the point of divergence of the cotyledons, the bases of the petioles form a continuous collar around the epicotyl enclosing

the growing point and the primordia of the first foliage leaves. (Fig. 236.) When the petiolar bases diverge, each is crescentic in transection. In the lamina of the cotyledon, the mesophyll is differentiated into palisade and spongy parenchyma. The palisade cells are not as elongated as in the foliage leaf, but they do form a distinct layer beneath the adaxial surface that is more compact and has fewer intercellular spaces than occur in the five or six layers of spongy tissue.

ANATOMY OF THE STEM. — The fleshy crown stem of the first year constitutes the so-called "heart" of celery. It has a large

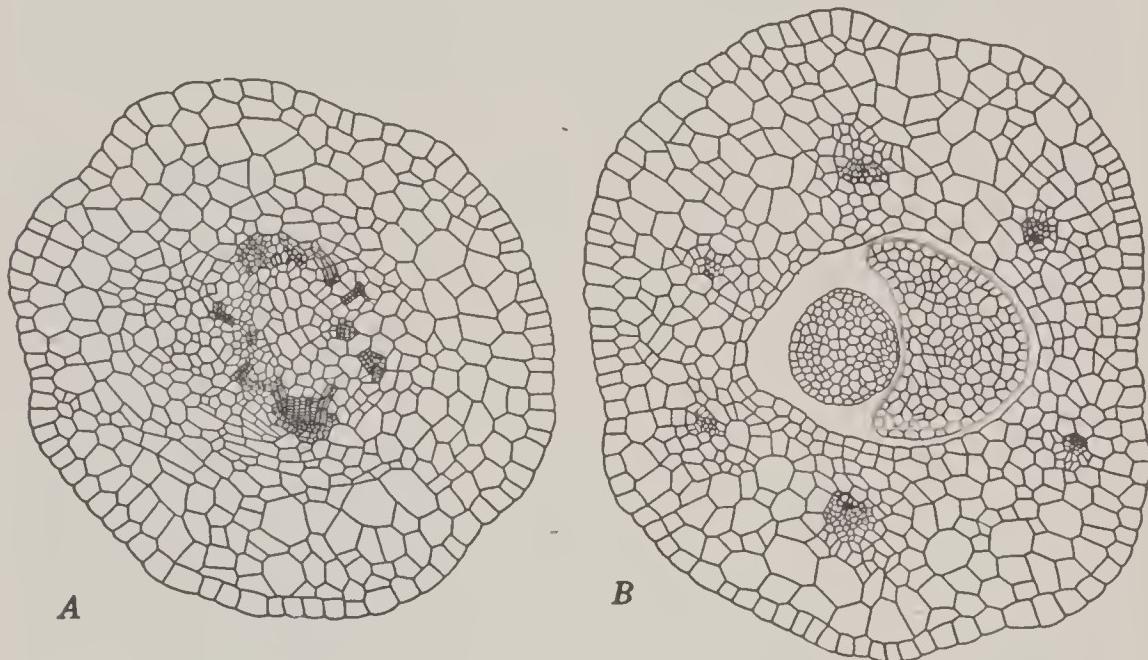


FIG. 236. *A*, transection of upper hypocotyl showing divergence of six cotyledonary bundles. Two procambial strands of foliar bundles appear in the intercotyledonary plane; *B*, transection of seedling axis showing cotyledonary collar surrounding growing point of epicotyl and base of first foliage leaf. The xylem of median cotyledonary bundle is tangentially oriented rather than endarch at this level.

central pith, and oil ducts occur in the peripheral portion. Associated with them are numerous medullary bundles which lie centrad to the vascular ring. The occurrence of medullary bundles in the Umbelliferae is not constant, but has been reported by Solereder (22) for sixteen genera, including *Apium*. They do not occur in *Pastinaca* or *Daucus*.

At the periphery of the pith is an almost continuous cylinder of vascular tissue comprised of bundles of the leaves which form the rosette of the first year. The leaf traces constitute a ramifying network of vascular strands that continue through the cortex into the bases of the petioles. Because internodal elongation is very

limited, the leaf bases overlap one another in such a way that there is little exposed epidermal surface. Buds occur in the axils of the

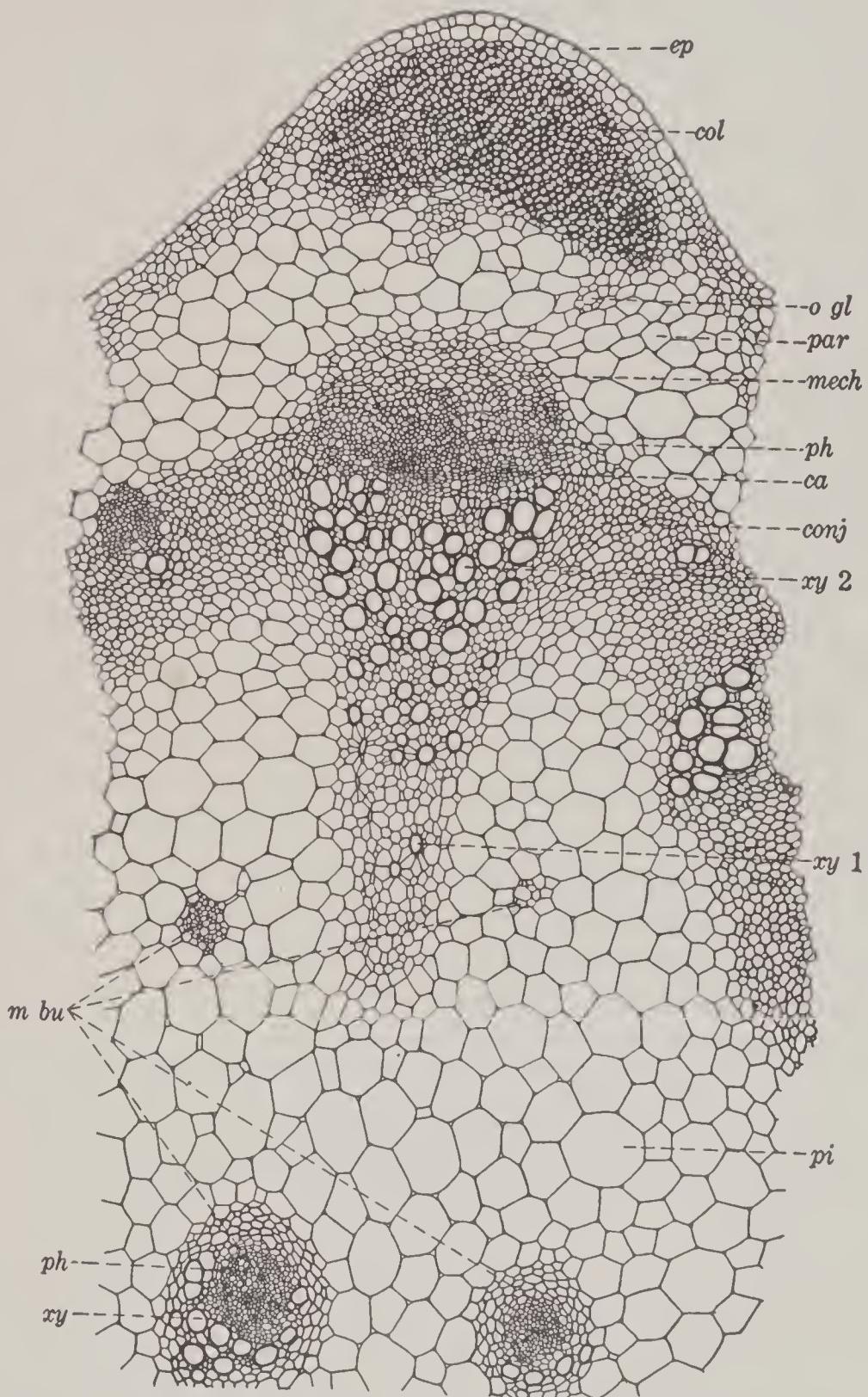


FIG. 237. Transection of mature stem showing sector of vascular cylinder and medullary bundles: *ca*, cambium; *col*, collenchyma; *conj*, conjunctive tissue; *ep*, epidermis; *m bu*, medullary bundles in various stages of development; *mech*, mechanical tissue; *o gl*, oil gland; *par*, parenchyma; *ph*, phloem; *pi*, pith; *xy*, xylem; *xy 1*, primary xylem; *xy 2*, secondary xylem.

leaves and their subsequent development results in the formation of the much branched shoot of the second year.

ANATOMY OF THE FLORAL AXIS. — The mature floral axis is strongly ridged and fluted and may or may not become hollow at maturity. The outer walls of the epidermis are thickened and covered with a somewhat roughened cuticle. Stomata occur in the portions of the epidermis overlying the chlorenchyma, and Nestel (16) has indicated their frequency at about 70 per square millimeter. The zone of chlorenchyma which lies within the epidermis, except at the angles, is four or five layers in width, and the round or elliptical cells are slightly longer than broad. The non-chlorophyllose parenchyma of the cortex consists of large cells that are more loosely organized than those of the chlorenchyma. (Fig. 237.) They occupy the region between the chlorenchyma and vascular cylinder, also separating the collenchyma from the large bundles located at the angles of the stem.

The strands of collenchyma constitute the chief mechanical tissue of the axis and form the ridges, being separated from the epidermis by one or two layers of parenchyma which later become thick-walled. These cells are larger in transection than the collenchymatous elements; and, in longisection, can be distinguished from them since they are only two to three times as long as broad with transverse end walls, while the collenchymatous cells are much elongated and sharply pointed or oblique. Additional strands of collenchyma also may be located in the grooves between the ridges, and these are separated from the epidermis by chlorenchyma rather than by thick-walled parenchyma. The collenchymatous strands at the ridges are oval or kidney-shaped in transection, while those in the intervals are more or less circular. Centrad to each strand is an oil gland or duct, and similar ones commonly occur outside the phloem of each vascular bundle.

The vascular bundles are collateral, the larger ones lying on radii which pass through the angles of the stem. Nestel, in a comparative study of the stems of the Umbelliferae, points out that celery belongs to the type in which there is no interfascicular cambium. Because of this, the adjacent bundles are distinct from one another, except that the medullary rays are occluded on the xylem side of the ring. This results from the differentiation of the ray parenchyma to form connective or conjunctive tissue by lignification and wall thickening as the stem matures. The

libriform or connective type of cell also surrounds the inner face of the xylem of each bundle to some extent. The portion of the ray adjacent to the phloem does not mature as connective tissue, but the outer face of the phloem is capped by cells which tend to become thick-walled.

The xylem region consists of numerous vessels separated from one another by parenchymatous cells. The first-formed protoxylem elements are of small caliber with open spiral thickenings, while those that mature later are larger with much closer spirals. A rather striking feature of the spiral wall thickenings is that in many cases the bands are double. The vessel segments of the metaxylem have very close spirals or a reticulum.

One or more ducts are developed in each primary phloem group, and there are three in most of the larger bundles that subtend the angles of the stem. Two or three occur in bundles of intermediate size and there is a single duct in the small bundles. The smaller secretory canals located in the peripheral portion of the pith are bounded by five or six epithelial cells. The fascicular cambium is relatively inactive, producing a limited amount of secondary xylem and phloem; but at the nodes, there is more activity and the nodal plate may become considerably lignified owing to the development of secondary xylem consisting of pitted vessels, fibers and parenchyma.

MEDULLARY BUNDLES. — Medullary bundles are distributed in the peripheral portion of the pith, and in a given stem, may be found in several stages of development. In most cases, the phloem is well developed, while the extent of xylem formation is variable. The bundle may be completely amphivasal, half-amphivasal, or collateral, and types are found in which the bundle appears to be bicollateral with xylem on two sides of the intervening phloem. The more completely developed bundles, regardless of type, are surrounded by sheaths of wood parenchyma. (Fig. 238.)

In most instances, an oil duct is centrally located in the medullary bundle and the phloem is arranged in concentric layers around it. Outside the phloem, the xylem is variously distributed or may be entirely lacking. Preliminary investigations indicate that the ontogeny of the medullary bundle is related to the secretory canals, and it appears that they are initiated by an activation of cells adjacent to the epithelial cells which line the duct. (Fig. 238, A.) These cells form a meristematic strand by a series of periclinal

divisions which proceed until there is a strand several cell layers in width surrounding the duct. (Fig. 238, D.) They later differentiate as the xylem and phloem elements of the mature medullary bundle.

Medullary bundles are not restricted to the Umbelliferae, but as noted by Wilson (31) are found "in a large number of unrelated

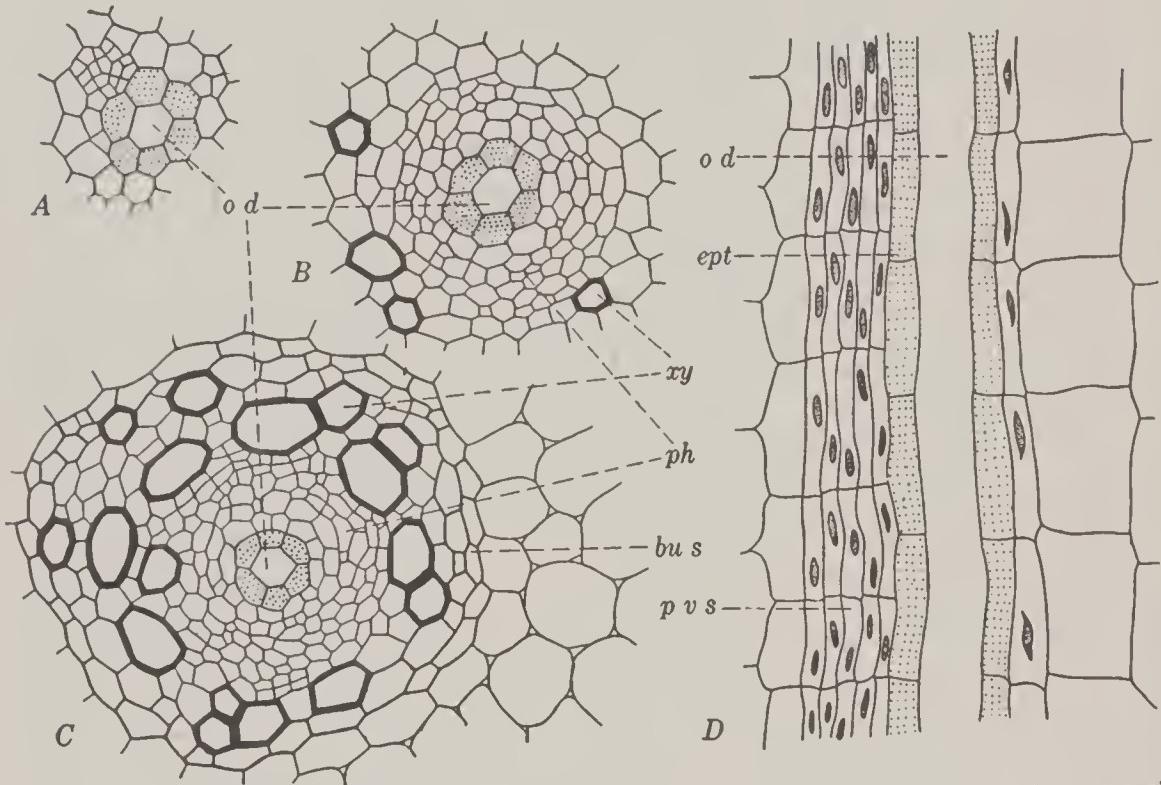


FIG. 238. Medullary bundles: A-C, stages in development of bundle showing central oil duct and amphivasal arrangement of vascular tissues; D, longisection of portion of oil duct showing formation of provascular strand adjacent to epithelial cells of duct: *b u s*, bundle sheath; *e p t*, epithelial cells; *o d*, oil duct; *p h*, phloem; *p v s*, provascular strand; *x y*, xylem.

families, perhaps thirty or more." The term "medullary bundle" has been variously applied by those who have described these structures. They were considered by Weiss (29) and Col (5) to be common rather than caudine in most instances, and were regarded as the extensions of leaf traces instead of an independent system of stem bundles. Westermaier (30), working with species of *Begonia* which have tubers or rhizomes, suggested that the medullary bundles are supplementary to the usual ring of vascular bundles. In *Apium*, it appears that the medullary bundles arise early in ontogeny of the stem and may be traced to the ultimate branches of the umbel. It seems probable that they are caudine, supplementing the common bundles in the translocation of materials during the period of flowering and fruit development. They may

compensate for the absence of an interfascicular cambium which, when present, serves the purpose of adding secondary vascular elements to the conducting system of an axis. Nestel (16) has reported rare instances in which there were small isolated bundles in the cortical parenchyma. These were amphicribral in contrast with the amphivasal condition found in medullary bundles.

ANATOMY OF THE PETIOLE. — The petioles of the leaves of the first year constitute the principal edible part of the plant, and the marketability of celery depends upon their quality. Sayre (20) has pointed out that the desirable characteristics are crispness, tenderness, the absence of strings, and a pleasant, sweet, nut-like flavor. Undesirable qualities which decrease marketability are pithiness, toughness, stringiness, and a rank or pungent flavor.

Several of these characters are definitely related to structure, and this has focused attention upon the developmental anatomy of the petiole. Norton (17) has stated that "Quality in celery is primarily a question of the proportional relationships of the so-called parenchymatous tissue to the fibrous tissue," and he attributes the differences in quality, aside from those that are hereditary, to external factors including soil moisture, plant food, especially nitrates, rate of growth, light, and temperature. Mills (14) regards high quality as being determined by flavor, which he thinks is associated with the chlorophyll content in the stalks, and by degree of crispness, which he relates to the water content in the plant. He notes that lack of crispness may be the result of excessive temperature, too much or too little moisture, nitrogen deficiency, and excessive retardation or acceleration of the growth rate. Like other investigators, he attributes part of the pithiness to heredity, pointing out that some varieties of celery develop this undesirable characteristic more frequently than others.

Thompson (23) has noted that storage conditions may affect crispness, especially insufficient moisture and too high temperature, which result in over-rapid maturation and pithiness. Sayre (20) investigated eight varieties of celery to determine the anatomical factors which might have a bearing upon stringiness and toughness, concluding that

"The only celery tissue that seemed to have a very definite relation to stringiness was the collenchyma," and "pithiness is evidently correlated with a breaking down of the parenchyma cells which leaves large open spaces through the center of the stalk."

More recently Esau (7), who attacked the problem by comparing the relative mechanical properties of the collenchyma and vascular tissues, concluded that "Mechanically the collenchyma

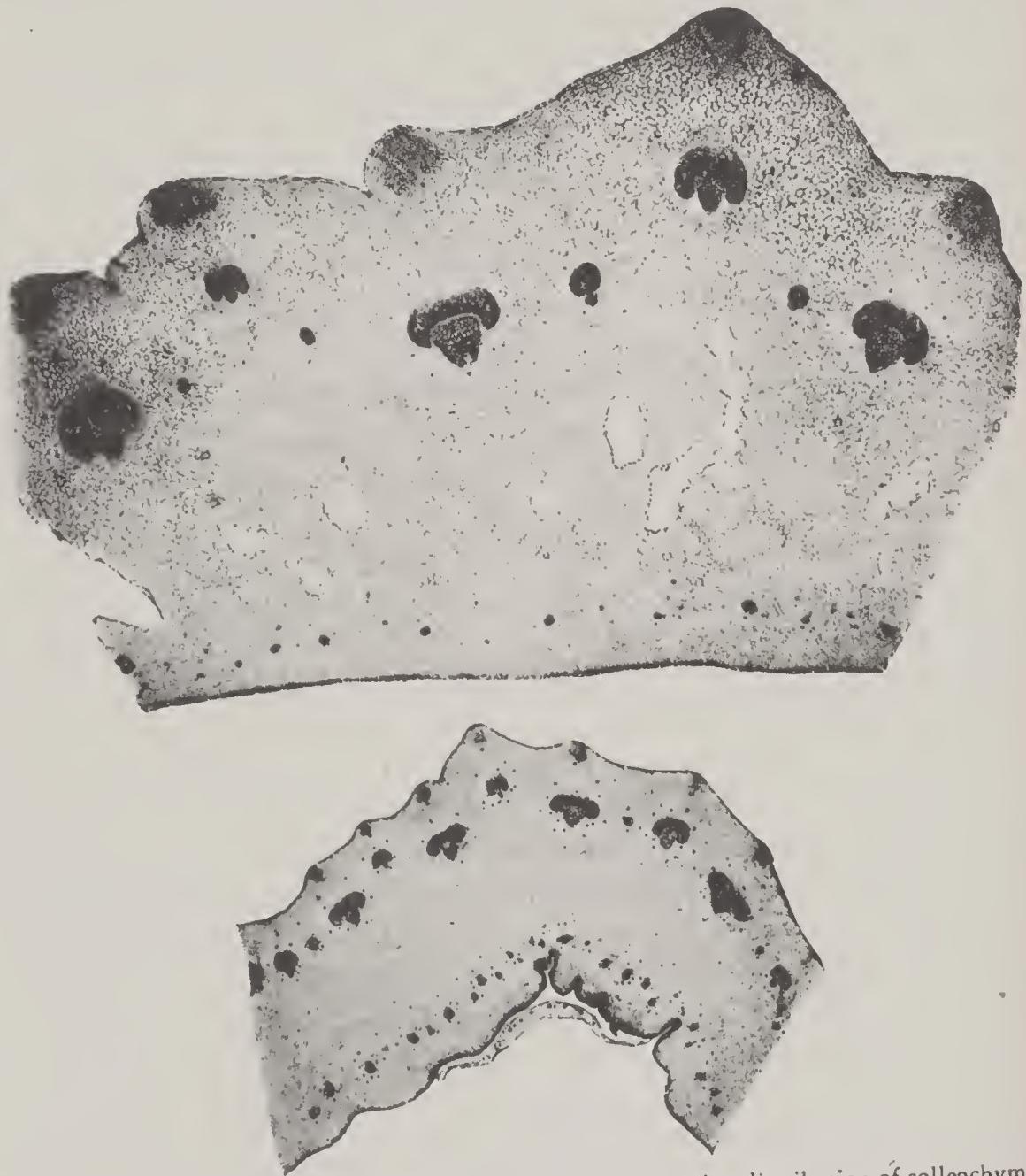


FIG. 239. Upper, transection through mature petiole showing distribution of collenchyma and vascular bundles. Schizogenous lacunae have developed in parenchyma. Lower, transection of somewhat less mature petiole showing same features except for absence of lacunae. In both figures, the abaxial surface is upward. (Photomicrographs by Esau, *Hilgardia*.)

is much stronger than the vascular tissue. The breaking load of collenchyma may be two to four times that of the entire vascular bundles or the bundle cap."

In transection, the crescentic petiole is broadly expanded at its base and more subcylindrical above with an adaxial groove extend-

ing to the point of divergence of the lower leaflets. The central axis of the compound lamina and the stalks of the lateral leaflets are also subterete with a grooved adaxial surface. The abaxial surface is prominently ridged, owing to the underlying strands of collenchyma, while the adaxial one is smooth and without reinforcing strands of collenchyma although there are usually two or more layers of thick-walled subepidermal parenchyma. The winged margins of the petiole are also strengthened with mechanical tissue.

The mesophyll is parenchymatous with large intercellular spaces. In plants that tend to be pithy, the parenchyma breaks down schizogenously at various points, leaving irregular internal cavities. (Fig. 239.) The number and distribution of the chloroplasts depend upon the variety and cultural methods practiced with respect to blanching. In most types, there is a zone of chlorenchyma immediately within the epidermis, except at the ridges and on the adaxial surface, and it also frequently surrounds the vascular bundles.

The principal vascular bundles lie in a semicircle immediately inside the collenchymatous strands with their phloem caps directed toward the abaxial surface. Between the major bundles, there may be smaller ones, their number and orientation depending upon the variety of celery and the level at which the transection is taken. A row of small adaxial bundles may occur, these being more evident at the base of the petiole than at its upper limits. (Fig. 239.) At intermediate levels, the smaller bundles occupy a more nearly central position in the mesophyll; and, above, they come to lie approximately in the abaxial ring. As reported by Esau (7), they may consist of phloem only; in some instances solitary xylem cells have been noted; and, in others, there are bundles in reverse orientation in which the phloem of the adaxial bundles is directed toward the adaxial surface.

Numerous oil ducts occur in the phloem, prominent ones lying centrad to each collenchymatous strand and outside the phloem caps of the larger bundles. They are also generally distributed throughout the parenchymatous tissue adaxial to the main vascular ring. (Fig. 240.)

The walls of the epidermal cells are thickened, especially the outer one over which there is a well-defined cuticle. There is considerable irregularity in the shape of these cells, as seen in

surface view; but, in general, they are quadrangular and their greatest dimension is parallel to the long axis of the petiole. Stomata occur on both surfaces, being more numerous on the abaxial one where they are arranged in approximate rows in the furrows. The stoma is of the type in which the initial epidermal

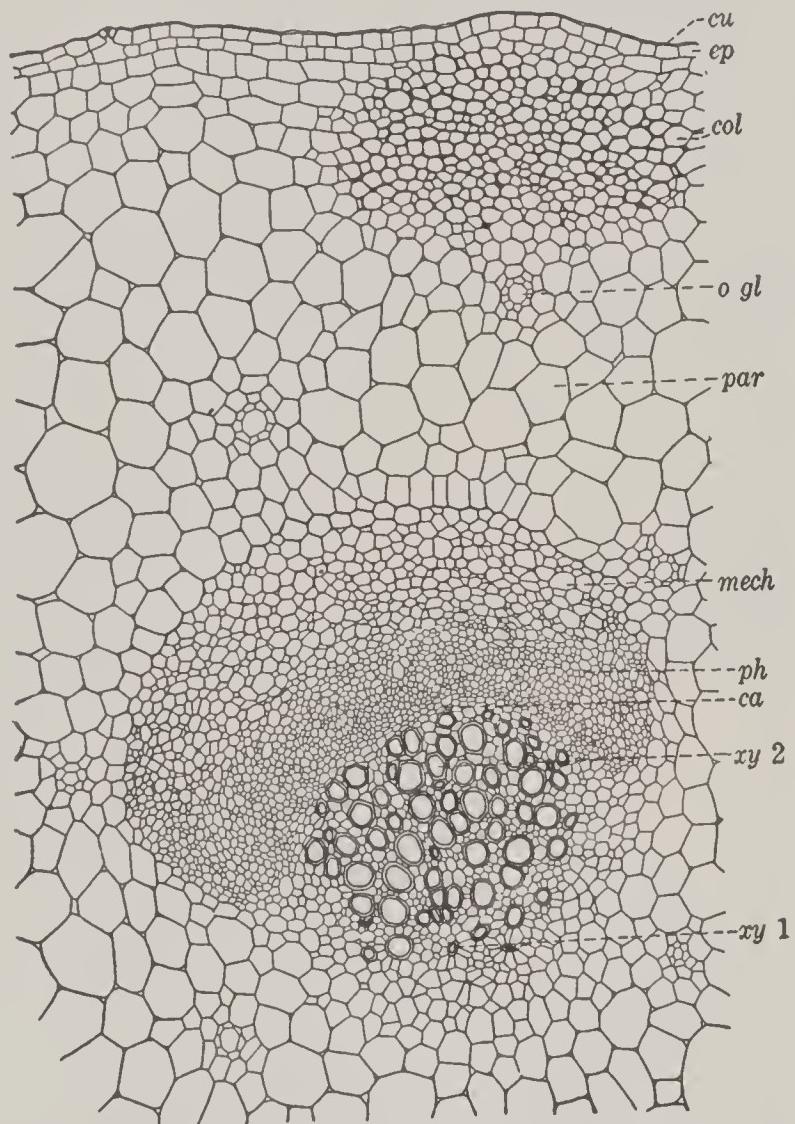


FIG. 240. Transection of sector of petiole showing vascular bundle and location of mechanical tissue underlying abaxial epidermis: *ca*, cambium; *col*, collenchyma; *cu*, cuticle; *ep*, epidermis; *mech*, mechanical tissue; *o gl*, oil gland; *par*, parenchyma; *ph*, phloem; *xy 1*, primary xylem; *xy 2*, secondary xylem.

cell is not the mother cell. In its development, the initial cell is divided successively so that two or three accessory cells are formed surrounding the mother cell. A final division of the mother cell results in the two guard cells. (Fig. 6.)

ONTOGENY OF THE LEAF. — The ontogeny of the leaf is similar to that described by Sachs (19) for *Pastinaca* and other Umbelliferae. It first appears as a cone-shaped primordium which

"quickly broadens into a shell-like form, and grows vigorously at its apex. Beneath the apex, protuberances arise at the right and left angles in acropetal order; these also grow in the same manner at their apex, and produce again lateral protuberances of the second order; and according to the extent to which the surface of the leaf is developed, these protuberances become lobes of a simple leaf or distinctly separated leaflets." (Fig. 31, A, B, C.)

Esau (7) has described in detail the histogenesis of the petiole in which there is an early differentiation into three meristematic regions, the protoderm or dermatogen which gives rise to the epidermis, the procambium which produces the vascular strand, and the ground meristem which becomes the fundamental parenchyma. The cells of the three meristems can be distinguished early in ontogeny by their size, degree of vacuolation, and the character of the cell divisions which they undergo. The cells of the ground meristem are the largest and the first to develop prominent vacuoles and intercellular spaces. The small protodermal cells are more dense than those of the ground meristem; and the procambial cells are the least vacuolate and smallest in transection of the three types, but are longer than the others in their axial dimension. The cells of the protoderm divide only anticlinally, producing the epidermis and stomatal cells. The ground meristem divides in three planes, but the divisions are less frequent than in either of the other histogens, and they compensate in part for this by more rapid cell enlargement.

The procambial tissue arises in the ground meristem through a series of rapid periclinal longitudinal divisions, and the strands which are the forerunners of the larger bundles are differentiated in this manner earlier than those which form the smaller intervening bundles and the adaxial ones.

According to Ambron (1) the strands of collenchyma differentiate from the procambial tissue, later becoming separated from it through the differentiation of an intervening layer of parenchyma. This is not in agreement with the work of Esau (7), who finds that the collenchyma and the vascular bundle have independent origins, and that they are clearly set apart from each other. Their separate origin is emphasized by the early differentiation of an oil duct which lies in the parenchyma between the collenchyma strand and the bundle cap outside the phloem. (Fig. 241.)

DEVELOPMENT OF THE COLLENCHYMA. — The mature collenchymatous cells are small in transection and very much elongated

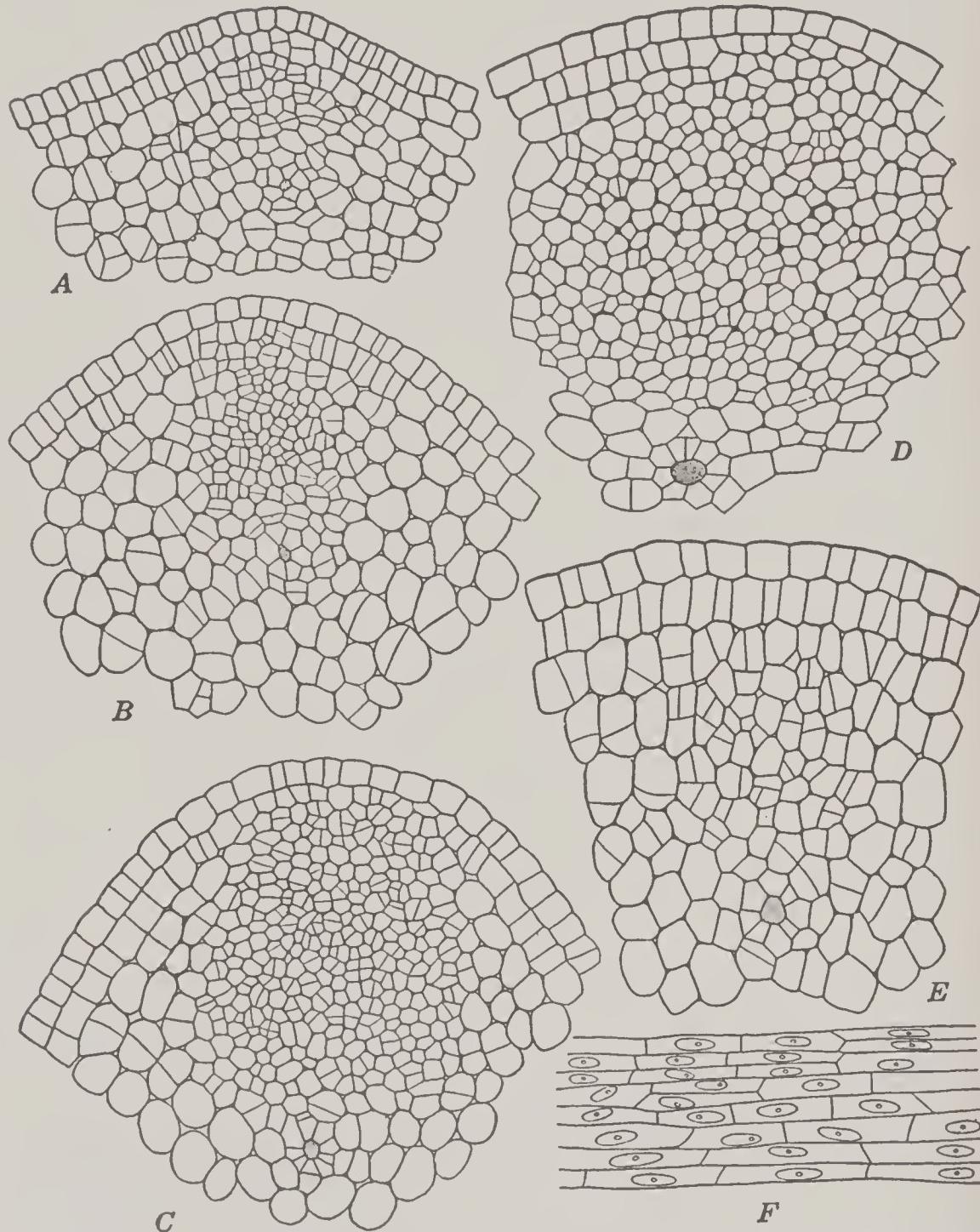


FIG. 241. *A-D*, transections of collenchyma in successive stages of development; *E*, stage showing late initiation of collenchyma; *F*, longisection of young collenchyma. Stippled areas represent oil ducts. (After Esau, *Hilgardia*.)

axially with oblique end walls. The walls are thickened chiefly at the angles, although there are some additional thickenings on the lateral surfaces. (Fig. 241.) The development of the young strand at first resembles that of a procambial one; and longitudinal,

periclinal, and later anticlinal divisions result in the formation of a large number of much elongated cells with small diameters. The strand continues to increase in size through repeated divisions of the cells of the strand itself, and through the addition of peripheral cells derived from the adjacent fundamental parenchyma. The divisions occur so rapidly in the early ontogeny of the collenchyma that the resultant cells are much smaller than those of the surrounding tissue.

Cell enlargement does not begin until cell division is slowed down, at which time the deposition of the characteristic wall thickenings is initiated. In their meristematic condition, the young collenchymatous cells are longer than wide with transverse or slightly oblique end walls which become more tapering as growth proceeds. In later stages of development, thin transverse walls may be laid down. The mature cells retain their protoplasts and their potentiality for growth and enlargement. The walls are chiefly cellulose with a high percentage of water, but they also contain pectic substances which are more abundant near the middle lamella.

Anderson (2) has found that the cellulose and pectic substances of the collenchyma occur in alternate layers and has suggested that this alternation may help to explain the fact that contraction in the transverse plane is much more pronounced than in the longitudinal one. He points out that this also may account for the high percentage of water found in the walls of the collenchyma, which greatly exceeds that found in those of lignified cells.

ONTOGENY OF THE BUNDLE. — The vascular bundles are endarch and collateral. At maturity each consists of a xylem region which is oriented toward the adaxial surface and a phloem zone which partially surrounds the abaxial face of the xylem so that the bundle may be half-amphicribral. The walls of the outermost phloem cells thicken to form a strengthening cap on the abaxial face of the bundle. A weak cambium may be formed, but the amount of secondary tissues cut off by it is relatively small so that the major portion of the vascular tissue can be regarded as primary.

In the ontogeny of the bundle, the procambial strand gives rise to protoxylem and protophloem cells which are located rather near to each other; but, according to Esau,

"continued division of procambial cells in the center of the bundle increases the distance between them. The procambial cells formed

centrifugally from the xylem differentiate into new elements of this tissue, while new phloem cells arise on the opposite side of the bundle. Since, however, the differentiation of elements progresses faster than the division of procambial cells the xylem and phloem gradually approach each other." (Fig. 242.)

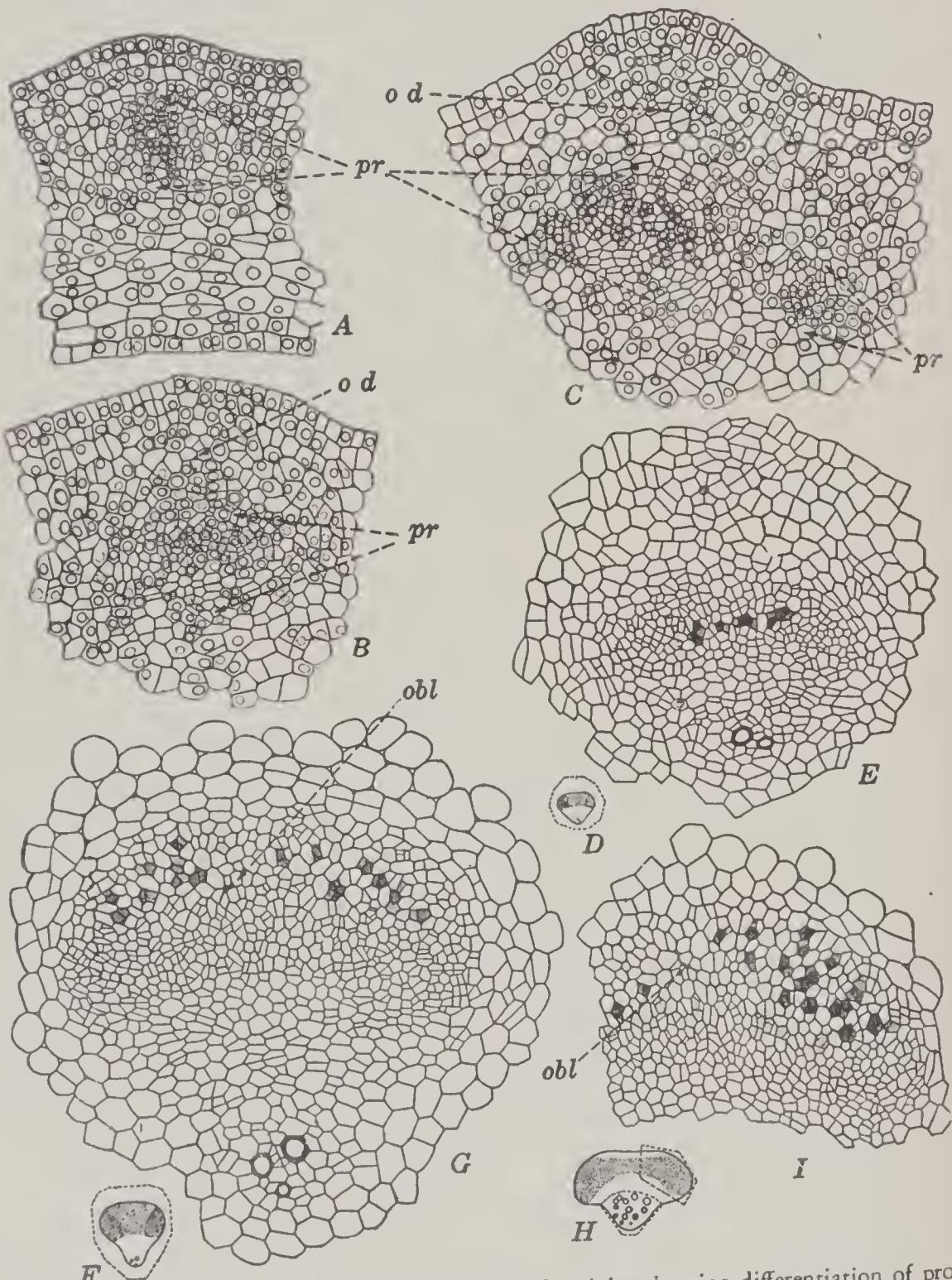


FIG. 242. A-C, transections through portions of petioles showing differentiation of procambial strand; D, E, G, I, transections showing early differentiation of vascular tissue; F, H, diagrams of entire bundles from which drawings E, G, I were made: *obl*, obliterated phloem; *od*, oil duct; *pr*, procambium. (After Esau, *Hilgardia*.)

The narrow layer of procambial cells which finally separates the primary xylem and phloem is the region which may form the cambial-like zone referred to above.

During elongation, only protoxylem and protophloem elements are matured; but when the petiole ceases to elongate, the procambium gives rise to metaxylem and metaphloem elements. In most bundles, this completes the maturation, since little or no secondary tissue is present in the petioles.

ONTOGENY OF THE XYLEM. — The xylem tissue of the bundle consists only of vessels and parenchyma, no fibers being formed.

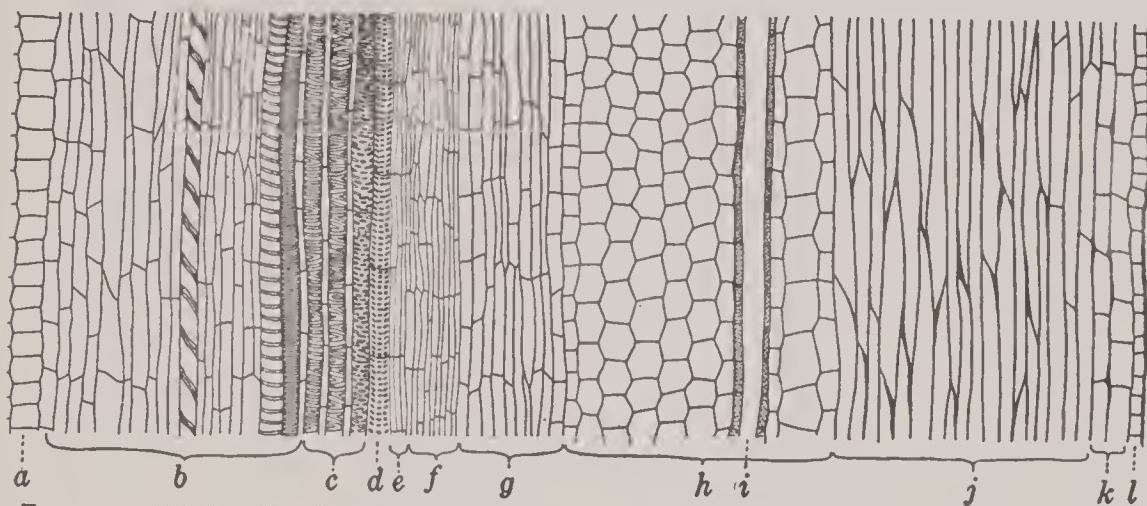


FIG. 243. Median longisection through bundle and adjacent tissue of petiole: *a*, pith; *b*, protoxylem, including spiral vessels and parenchyma; *c*, metaxylem; *d*, pitted secondary xylem vessel; *e*, cambium; *f*, phloem; *g*, bundle sheath; *h*, cortical parenchyma; *i*, cortical oil duct with epithelial cells; *j*, collenchyma; *k*, thick-walled parenchymatous cells; *l*, epidermis with cuticle.

The first-formed protoxylem elements are small in diameter, and the majority of them have secondary thickenings of an open spiral type, although infrequently there may be a limited production of vessels with annular bands. As the bundle elongates, the spirals become more and more stretched and some of the protoxylem elements are finally obliterated. The progressively larger metaxylem elements are scalariform and reticulate. There is a large amount of parenchyma adjacent to the protoxylem, and a limited number of parenchymatous cells surround the metaxylem vessels. (Fig. 243.)

In Esau's (8) study of vessel development, it is pointed out that the vessel segments expand very rapidly; and, in so doing, affect the spatial relationships of adjacent cells. These are not only flattened and distorted; but, in some cases, actual tearing of tissue may occur so that "new contacts are made by the expanding

vessel." When the vessel segment reaches its full diameter, it still contains its protoplast, the longitudinal walls are thin, and

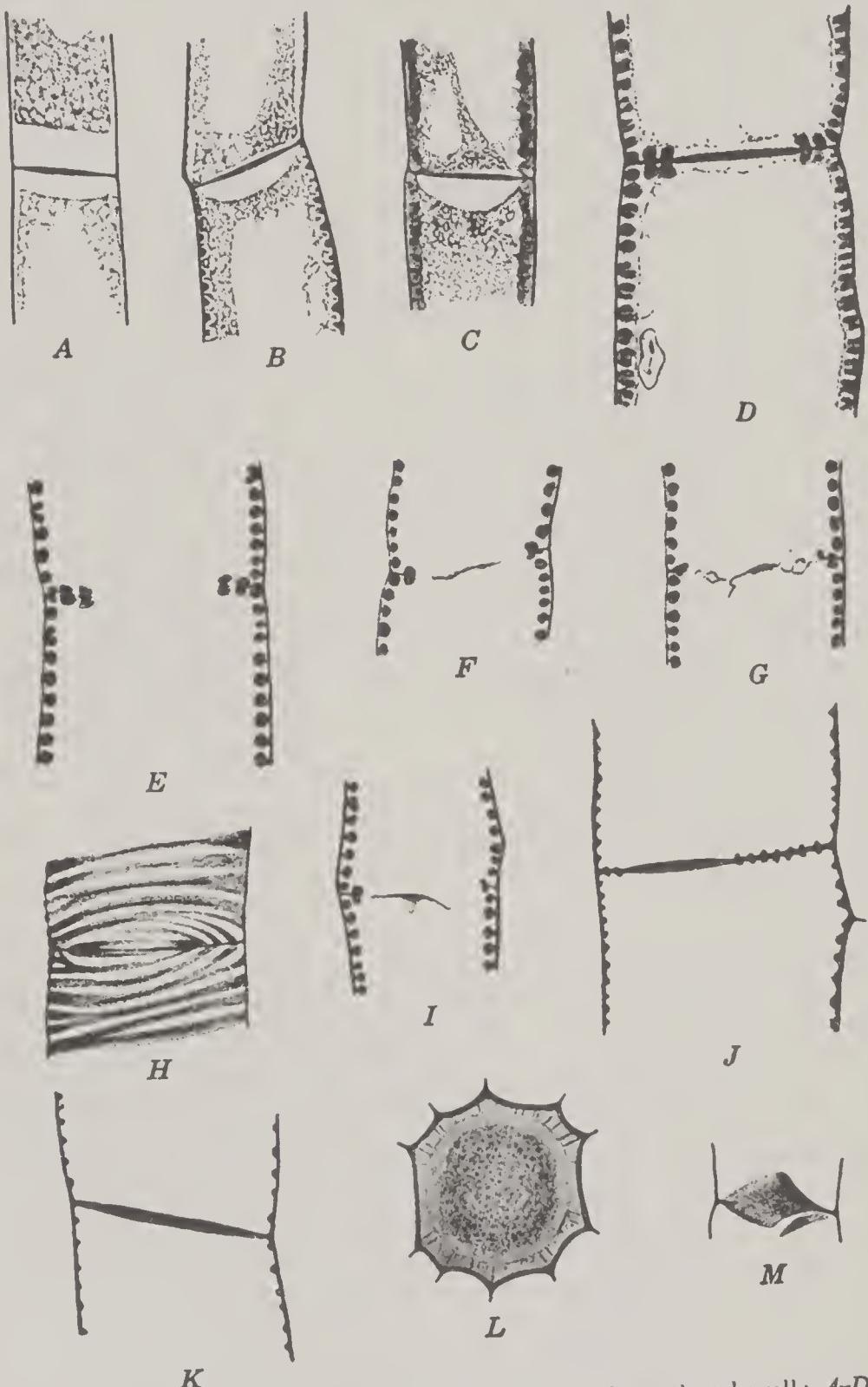


FIG. 244. Stages in development and disintegration of vessel end wall: A-D, stages showing thickened end wall and formation of spiral secondary thickenings; E, H, rim between two mature vessel elements shown at two different focal planes; F, G, I, stages in disintegration of end wall; J, end wall of vessel elements which in mature state communicate through small perforation; K, median line in thickened end wall; L, end wall in face view; M, end wall broken in preparation. (After Esau, *Hilgardia*.)

the end walls are characteristically thickened. (Fig. 244, A-C.) These thickenings are lenticular, occurring only on the portion of the wall which is later removed during the maturation of the vessel, while the remainder of the end wall is thin. After the end wall has thickened, the vessel segments develop secondary wall thickenings of the spiral, scalariform, or reticulate types which are deposited on the longitudinal walls and also on the thin portion of the end walls. The disintegration of the end wall of the vessel segment occurs when the longitudinal secondary wall is mature and the protoplast is beginning to disappear. (Fig. 244, F, G.) At this time, the lenticular portion of the end wall becomes thinner until finally it completely disappears, indicating that the process is one of dissolution.

ONTOGENY OF THE PHLOEM. — The protophloem consists of sieve tubes and companion cells, each tube having one of the latter. (Fig. 245.) As development proceeds, some of the first-formed protophloem is obliterated by crushing and additional sieve tubes are formed centripetal to them. The metaphloem has less parenchymatous tissue; and the sieve tubes, though similar in structure to those of the protophloem, are larger. Each tube usually has one companion cell, but sometimes there are two short ones. (Fig. 245, G.)

In the formation of the protophloem, the procambial mother cell divides several times. The next to final division forms a parenchymatous cell and the mother cell, after which a longitudinal division of the latter produces a sieve tube and companion cell. In the development of the metaphloem, some of the parenchymatous cells may develop directly from procambial cells; but, in most instances, a procambial cell divides longitudinally. One daughter cell becomes a parenchymatous cell and the other, the mother cell of a sieve tube and companion cell. In the division of the mother cell, the larger of the daughter cells forms the sieve tube.

In maturation, the sieve tube first develops thickenings on the longitudinal walls, and the sieve plate thickenings occur later at about the time that the nucleus disintegrates. The wall thickening appears to be uniform on all longitudinal walls, but the one adjacent to the companion cell may or may not be thickened. In old age, prior to obliteration, the walls of the sieve tube lose their thickening, and this is followed by crushing as a result of the growth and enlargement of adjacent parenchymatous cells.

The bundle cap subtending the outer, abaxial face of the phloem is composed of enlarged parenchymatous cells whose walls have

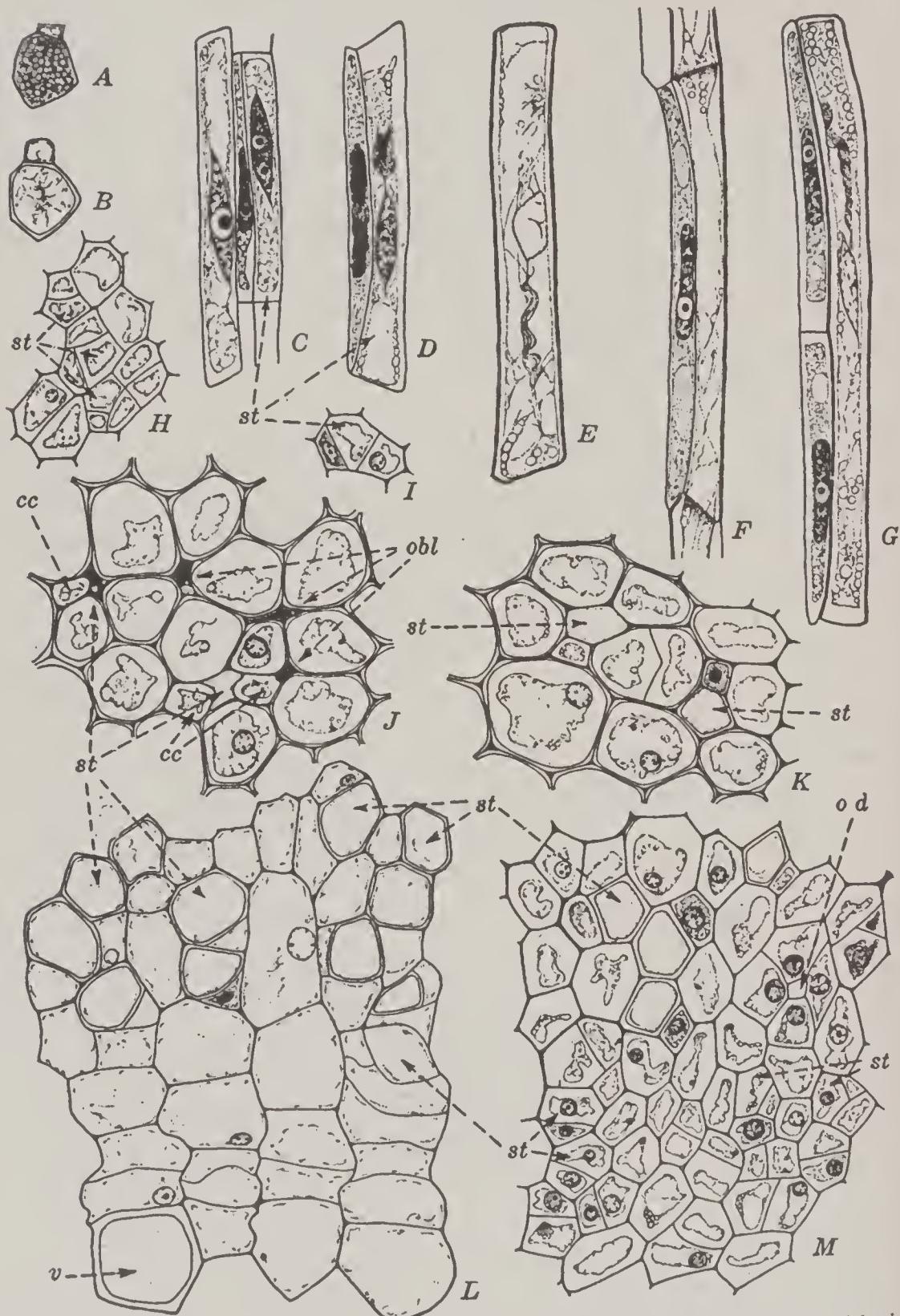


FIG. 245. Details of phloem structure: A, B, two transections of a sieve tube with sieve plate in A; C-G, stages of sieve tube differentiation shown in longisection; H-M, stages of phloem development shown in transection: cc, companion cell; obl, obliterated tissue; od, oil duct; st, sieve tube; v, vessel. (After Esau, *Hilgardia*.)

thickened. These cells retain their protoplasts; and, as they mature, the end walls, which are at first transverse or slightly oblique, become more tapering. The wall thickening consists of cellulose, and its distribution resembles that of collenchymatous cells. (Fig. 243.) The obliteration of sieve tubes and companion cells is the result of active growth of the phloem parenchyma, and the same displacement of cells may occur which has been noted in the growth of the xylem vessels.

OIL DUCTS. — Oil ducts occur in both the protophloem and metaphloem, and their formation in this region, as well as in the pith and cortex, is schizogenous. They are commonly formed by the development of an intercellular space at a point where three cells are in contact. The schizogenous splitting of the adjacent cell walls results in the formation of the duct, which is at first bounded by the three original cells but successive divisions of these cells may produce several epithelial cells. In the phloem, the schizogenous formation of intercellular spaces may occur so rapidly that additional cells are brought into contact with the duct by the separation of pairs of cells. The epithelial cells are densely cytoplasmic with large nuclei, and secrete an ethereal oil which accumulates in the duct. The duct is a continuous canal, and the epithelial cells surrounding it are arranged end to end in rows. (Fig. 243, I.)

MECHANICAL TISSUE OF THE PETIOLE. — The only tissues which contribute to the strength, and possible toughness or stringiness of the petiole, are the cells of the collenchymatous strands, the phloem elements which constitute the bundle cap, and the lignified elements of the xylem.

Esau (7) determined the relative breaking load of strands of these three tissues. In all cases, it was found that the collenchymatous cells were much tougher than those of either the xylem or the bundle cap; and that they also exceeded the combined strength of the last two tissues. This was not because of the size of the strands of collenchyma, for in many cases they were smaller than the entire vascular bundle, in some instances being thinner than the bundle caps alone. Differences in the strength of collenchyma were found in comparing varieties of celery; and tests indicated that the collenchymatous strands of Tall Golden Self-Blanching were weaker than those of Golden Plume, while some of the strands from an old leaf of the Utah variety were most tenacious. Varia-

tion was also noted in the breaking load when young collenchymatous strands were compared with older ones, the marked increase in toughness with increasing age of the tissue being correlated with increase in thickness of the cell walls.

THE LAMINA. — The blade of the much incised and compounded leaflet is relatively thin. The epidermal cells, as seen in surface

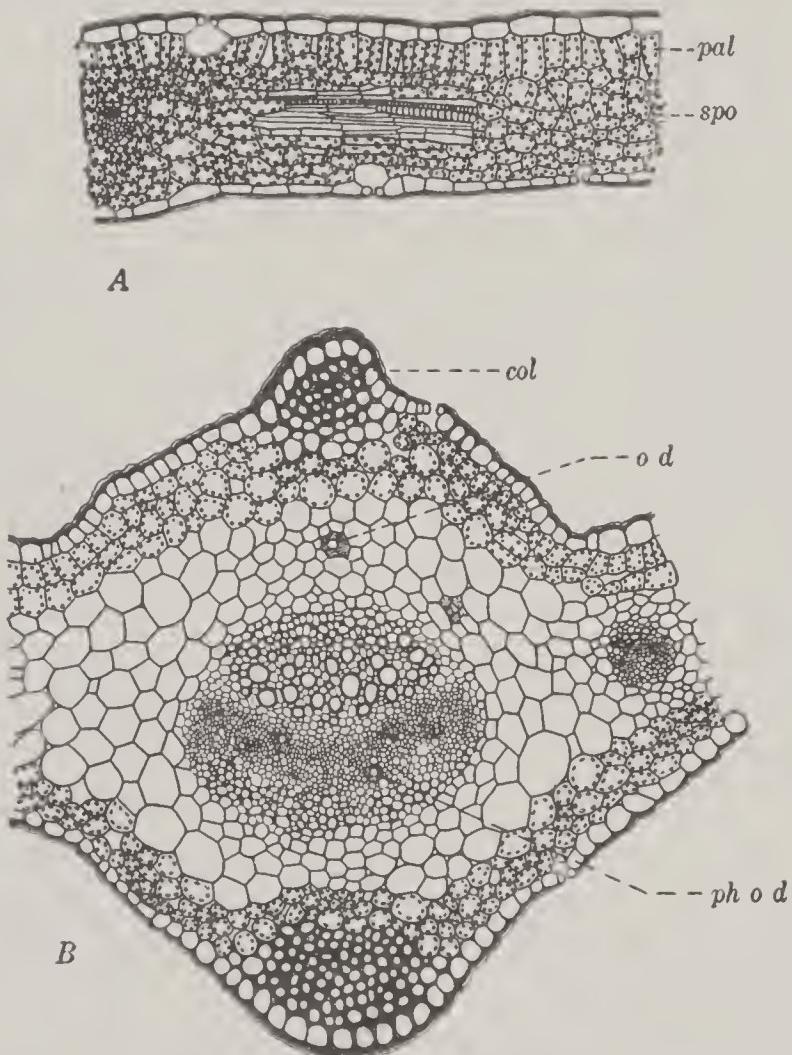


FIG. 246. *A*, transection of portion of lamina; *B*, transection through midrib of leaflet: *col*, collenchyma; *o d*, oil duct; *pal*, palisade cells; *ph o d*, phloem oil duct; *spo*, spongy parenchyma.

view, are of two shapes; those subtending the collenchymatous strands above the veins being rectangular with the elongated axis parallel to the vein, while those which overlie the chlorenchyma of the mesophyll have sinuous walls. The stomata occurring in this type of epidermis are bounded by two guard cells containing chloroplasts, and are surrounded by accessory cells as described for the petiole. The stomata occur on both surfaces, but are twice as numerous on the under one. Nestel (16) reports a count

of 200 per square millimeter on the under surface and approximately 100 per square millimeter on the upper one.

The outer walls of the epidermal cells are slightly thickened where the epidermis overlies the chlorophyll parenchyma, and very much thickened over the veins and at the leaf margins. The mesophyll consists of a single adaxial layer of palisade cells and four to six layers of spongy parenchyma which are rather compactly arranged. (Fig. 246, A.) The principal veins form projecting

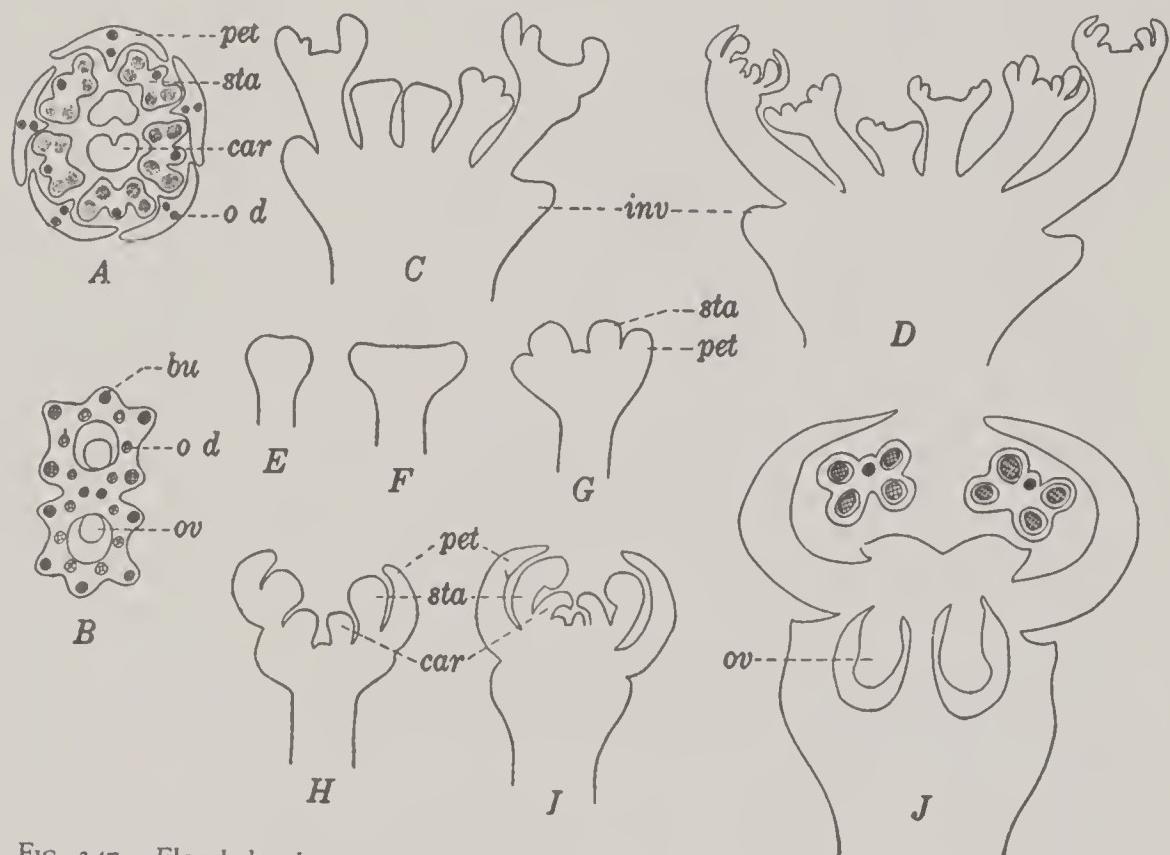


FIG. 247. Floral development: *A*, transection of young flower showing arrangement of parts; *B*, transection of young ovary with two carpels and ovules; *C* and *D*, early stages in formation of umbelliferous flower showing centripetal development of flowers; *E-J*, successive stages in ontogeny of individual flower (in *J*, filaments of stamens are not in plane of section): *bu*, vascular bundle; *car*, carpel; *inv*, rudimentary involucel of umbelliferous flower; *od*, oil duct; *ov*, ovule; *pet*, petal; *sta*, stamen.

ridges on both surfaces of the blade owing to the strands of collenchyma which lie immediately beneath the epidermis. The abaxial and adaxial strands are separated from the bundle by several rows of parenchymatous cells, and an oil duct lies above and below the vein. (Fig. 246, B.)

The vascular bundle resembles that of the petiole and is oriented with the xylem directed toward the adaxial surface. In the larger veins, the phloem cap is well developed and there is also

some thickening of the xylem parenchyma on the adaxial face of the bundle. The main bundles extend to the margin of the leaflet, where they terminate in conical projections, and the secondary veins form a reticulum with many cross-connecting veinlets.

FLORAL DEVELOPMENT. — The floral development of the Umbelliferae received early attention by many workers, including Payer (18), von Mohl (15), and Sieler (21). More recently, the subject has been investigated by Jurica (12) and Beghtel (4), the latter account dealing specifically with *Pastinaca*, which is similar to *Apium* in its floral ontogeny. The umbellets of the compound umbel develop centripetally so that the centrally located ones are the last to mature. This is also true of the flowers in each umbellet, where the peripheral ones are the first to develop. (Fig. 247, C, D.) The flower primordia arise from the broadened apex of the umbellet as club-shaped structures. The apex of each pedicel broadens and the primordia of the petals, stamens, and carpels arise in acropetal succession. (Fig. 247, E-J.) The involucel is rudimentary and does not develop, being represented in the young umbellet by a projecting fold of tissue. The flower is epigynous and the calyx is represented by a ridge at the summit of the inferior ovary. (Fig. 247, J.)

The primordia of the two carpels originate as independent crescentic structures which unite to form the two-loculed ovary. The pendulous, anatropous ovules are initiated before complete coherence of the carpels has been effected. In the development of the ovule, the nucellus arises from the placenta on the inturned edge of the carpel as a club-shaped structure which is at first straight. As growth continues, it begins to turn toward the outer wall of the ovary until it becomes completely anatropous. The funiculus is slender, and a single, thick, fleshy integument develops which completely encloses the nucellus. On the side next to the funiculus, the integument is scarcely recognizable because of the complete anaturity of the ovule.

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CHAPTER XVI

CONVOLVULACEAE

IPOMOEA BATATUS

THE sweet potato is the only representative of the Convolvulaceae that is of major importance as a food plant. Originally a native of tropical America and the West Indies, it is now cultivated in the South Atlantic and Gulf States, South America, Africa, Mediterranean Europe, India, Japan, the Malay Archipelago, Australia, and New Zealand.

The numerous varieties produced in the United States may be divided into two general groups. In one are the dry, mealy types such as Big Stem Jersey, Yellow Jersey, Early Carolina, and Triumph, which are much favored in the northern markets. The other group consists of those varieties in which the flesh is soft, moist, and sugary when cooked. These are preferred in the southern markets and include Nancy Hall, Georgia, Pumpkin Yam, and Porto Rico. The trade names used are subject to much change, since breeding and selection result in constant fluctuation in the number and names of commercial varieties.

GENERAL MORPHOLOGY

THE STEM. — For the most part, the sweet potato is a vine-like plant; but, according to Groth (2), the length of the stem may range from 2 feet in some bunch varieties to 20 feet or more in those of the liana type. In the latter, the stem may be strictly twining or may not twine at all. It is purple-green, or a mottled combination of purple, brown, and green; and varies in diameter from $\frac{1}{8}$ to more than $\frac{1}{4}$ of an inch at its largest part. Lenticels are abundant and there may be some degree of pubescence, hairs frequently being present on the young shoots which do not persist on the older stem. In prostrate vines, adventitious roots occur at each node.

THE LEAF. — The simple, entire leaves are spirally arranged with a $\frac{3}{5}$ phyllotaxy. There is a wide diversity of leaf form, and they may be cordate, hastate, slightly to deeply lobed, or cut. The apex and the lobes are acute or obtuse, the base is cordate to

truncate; and, in some instances, the midrib of the leaf or leaflet is prolonged beyond the blade to form a short awn-like structure. In general, the first leaves are cordate, while those formed later may be hastate, cut, or lobed. They are equally variable with respect to size, ranging from $2\frac{1}{2}$ to 6 inches in their greatest dimension. The venation is palmate, the veins forming more or less prominent projecting ridges on both surfaces.

The petiole varies from $2\frac{1}{2}$ to 9 inches in length. Its base may twine about a support to some extent, depending upon the variety, and it is commonly thickened, forming a cushion-like structure on the lower surface where it bends sharply upward. The adaxial surface is grooved and, on either side of the petiole and just below the

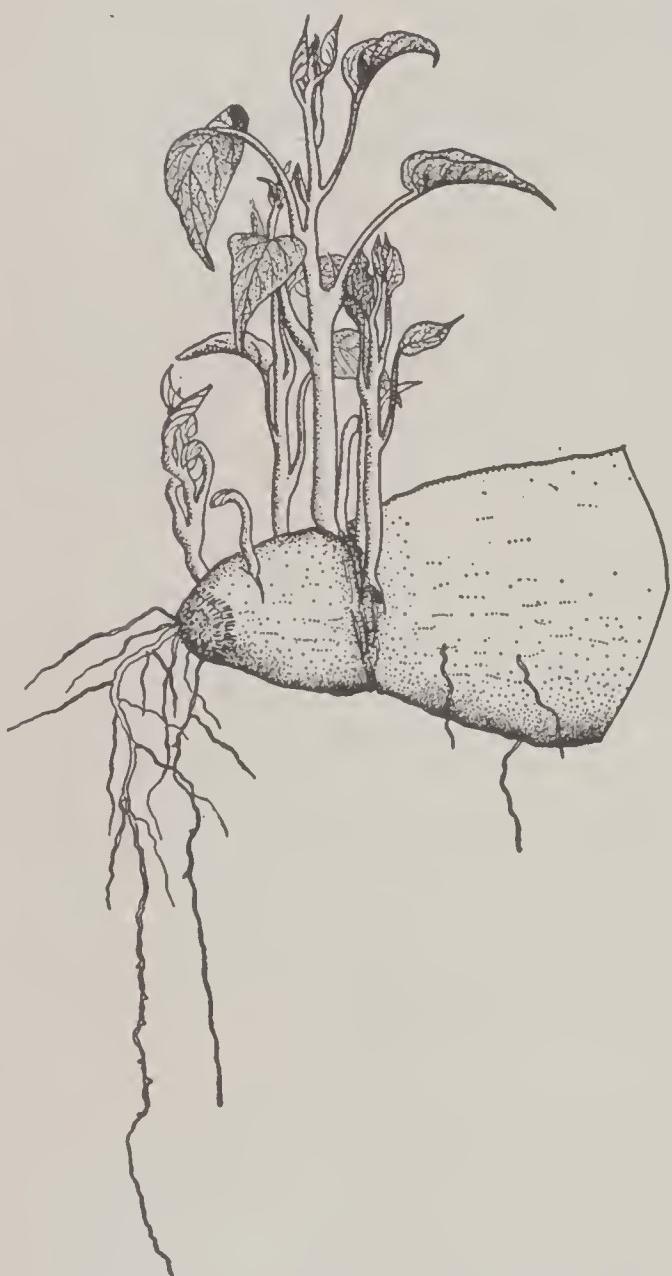


FIG. 248. The origin of young sprouts from fleshy root.

blade, there are two small petiolar nectaries. Glandular hairs occur on both surfaces but are more numerous on the abaxial one.

THE ROOT. — The root system is adventitious (except in plants grown from seed) and arises from fleshy roots, the stem, cuttings, or young sprouts known as "draws" or sets. (Fig. 248.) Isbell (5) has reported regeneration in leaf cuttings in which six different

types of sweet potato leaves were rooted and maintained under observation until the plants had formed shoots. The adventitious roots form a fibrous root system and some of them thicken greatly, the fleshy roots varying within wide limits from fusiform to napiform or nearly spherical. (Fig. 249.) Some are smooth and terete, others ribbed and more or less definitely four to six lobed in transection. Lateral roots arise from the deeply lobed roots in rows along the longitudinal grooves; and, in terete roots, each rootlet lies in a shallow recess surrounded by more or less loosened scar tissue. Kamerling (6) and Tuyihusa (14) maintained that these fleshy structures were stems rather than roots, but it is clear when the ontogeny of the structure is critically investigated that this concept is unwarranted.

THE FLOWER. — The production of flowers is relatively rare in continental United States, although Hand and Cockerham (3) report that the small, "morning-glory-shaped bloom, with a purple throat and white margin, may be noticed in commercial fields." In 1924 Stout (12) made a summary of the published records regarding seed production and concluded that seeds can be obtained from plants which produce flowers if there is proper cross-pollination. Blooming has been reported in all of the southern states where sweet potatoes are grown, but seed is seldom produced and in no instance has seed been matured in any quantity.

The plants flower profusely in the Virgin Islands, Puerto Rico, Cuba, Santo Domingo, Barbados, St. Vincent, Hawaii, the Philippine Islands, Java, and Australia. In many of these localities sufficient seed has been produced either naturally or as a result of



FIG. 249. Yellow Jersey sweet potatoes showing variation in shape and size. (Courtesy of the Bur. Plant Industry.)

artificial cross-pollination to permit the growing of seedlings. Experimental breeding has been carried on at the Virgin Islands since 1922, and a large number of seedlings have reached maturity. In 1925, the Virgin Islands Experiment Station reported that approximately 240 varieties had been grown in the preceding three-year period.

Thompson (13) describes the flower as follows:

"Usually, the flowers measure from $\frac{3}{4}$ to $1\frac{1}{2}$ inches in diameter, and the tube 1 to $1\frac{1}{2}$ inches in length. The color varies somewhat in the different varieties and, except in rare instances, is a shade of red, turning darker in the throat of the blossom. In 1100 seedlings examined there were two exceptions to this rule . . . bearing pure white flowers. Five stamens of varying lengths encircle the pistil and are attached to the inner surface of the corolla tube, near its base. The two longer ones either meet at or extend beyond the stigma, thus facilitating self-pollination. The pollen grain is spherical and bears many minute papillae which are symmetrically arranged upon its surface. The grain is 0.09 to 0.1 mm. in diameter. . . . The seeds are borne in a seed pod which is similar to that of the morning-glory, and range from 1 to 4 in a pod."

Natural crossing occurs readily and is probably carried on by hymenopterous insects, the most important of which is the honey bee. According to Thompson:

"The sweet-potato blossom opens only once. The bud opens during the night and remains open during the morning hours, then the corolla closes and withers. The time of closing of the blossom varies somewhat with the character of the day and the season. The flowers may remain open all day during cool, cloudy weather, especially in January and February, but they ordinarily close about noon on bright, warm days during this season. . . . In the latter part of April, closing of the flowers in the field on clear, warm mornings was observed to take place between 9 and 10 o'clock."

THE FRUIT AND SEED. — Under conditions in the United States, the sweet potato rarely produces viable seeds. Stout (12) concluded that sterility has been accentuated through the perpetuation of varieties having sterile tendencies for more than 400 years of vegetative propagation; that blooming requires a longer growing season than is necessary for the development of a crop of roots; and that some type of self-sterility or incompatibility operates to limit seed production even when environmental conditions favor blooming.

The fruit is a globose capsule usually consisting of a two-loculed ovary with two ovules in each cell. False septa may divide the locules so that the fruit appears to be a four-celled, four-valved capsule with a seed in each locule. The anatropous ovules are more or less basal and develop from axial placentae at the inner angle of each cell. The seed is approximately 3 mm. in its greatest dimension, black, somewhat flattened, with one surface angular and the other roughly convex. The seed coat is tough and corneous, and nearly impervious to water. The internal structure is similar to that described by Lubbock (9) for other species of *Ipomoea* and *Convolvulus*. The micropyle is deeply invaginated so that a tubular cavity is formed above the hilum and the inner portion of the seed coat is infolded to such an extent that the apical end of the seed is two-chambered. This septum probably determines the configuration of the two deeply bilobed cotyledons. (Fig. 250, A, B.)

As the embryo develops, the hypocotyledonary axis occupies the tubular cavity formed by the invagination of the micropyle. The development of the lateral lobes of the cotyledons, after the apex of each has come in contact with the intruded septum, results in the pushing of half of each cotyledon into one of the lateral chambers and the formation of well-defined auricles which lie on either side of the hypocotyl. As the cotyledonary lobes continue to grow, they become transversely folded. The dorsal and ventral aspects of the dissected embryo are shown in Figure 250, C and D. The seeds are albuminous and a pulpy endosperm overlies the folded cotyledons. Upon

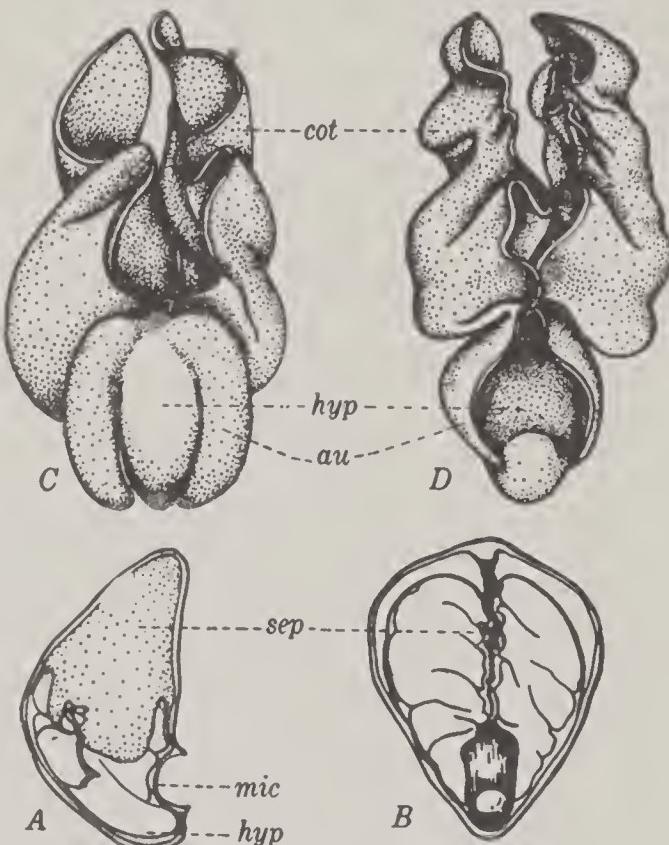


FIG. 250. A, median view of seed with portion of cotyledons cut away to show septum; B, ventral view; C, dorsal aspect of dissected embryo, after 24 hours; D, ventral aspect: *au*, auricle; *cot*, cotyledon; *hyp*, hypocotyl; *mic*, micropyle; *sep*, septum.

germination, this becomes mucilaginous and is absorbed by the cotyledons.

DEVELOPMENT OF THE SEEDLING.—Under greenhouse conditions, scarified seeds germinate rapidly.¹ The primary root emerges by the end of the first or second day, and subsequently there is a rapid elongation of the axis so that it may reach a length



FIG. 251. Stages in development of seedling; A, three days; B, five days; C, seven days; D, three weeks; E, first foliage leaf.

of 2 or 3 inches by the third or fourth day. There is an early differentiation of lateral roots, and by the fifth day, small branch roots can be seen at the upper root level. The hypocotyl elongates, carrying the cotyledons forward with it; and as they emerge from the soil and are liberated from the seed coat, the elongation of the cotyledonary petioles separates them from each other. The cotyledons are deeply bilobed, the lobes being obtuse or subacute, and the rounded auricles are rather prominent. Following the

¹ The seedling studies described in this section are based upon material grown from seed supplied by the Director of the Virgin Islands Experiment Station.

expansion of the cotyledons, the epicotyl begins to elongate and the first foliage leaves enlarge. In seedlings 21 days old there may be three or four foliage leaves which are simple, cordate at the base, and acute or pointed at the tip. (Fig. 251, A-D.)

ANATOMY

THE PRIMARY Root. — The primary root has a tetrarch protostele, and four groups of small phloem cells alternate with the

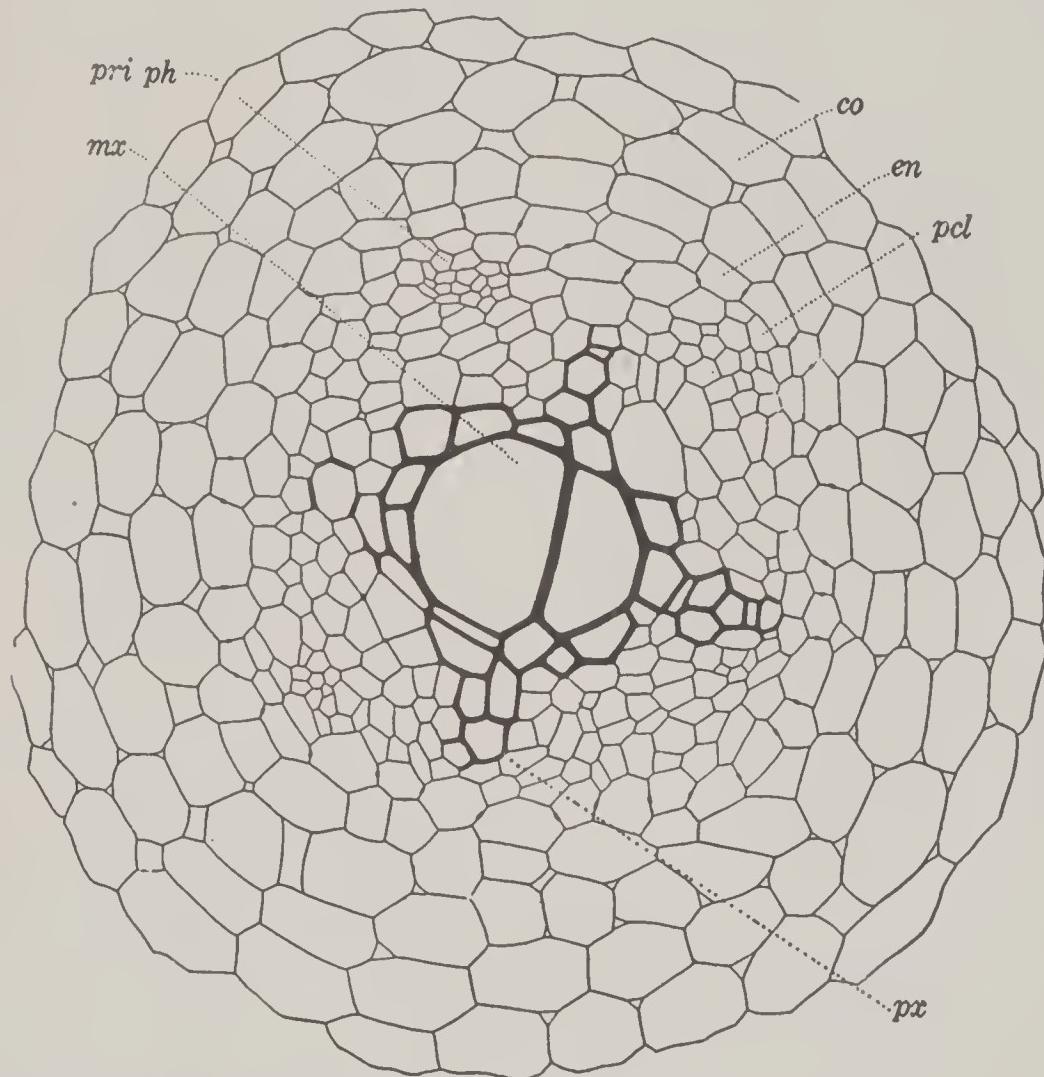


FIG. 252. Transection of young primary root: *co*, cortex; *en*, endodermis; *mx*, metaxylem; *pcl*, pericycle; *pri ph*, primary phloem; *px*, protoxylem. (After Artschwager, *Jour. Agr. Res.*)

primary xylem strands, being separated from them by fundamental parenchyma. (Fig. 252.) Each point consists of five or six protoxylem elements, the small outer ones abutting the pericycle while the larger inner ones lie adjacent to the centrally located metaxylem vessels. The cortex is limited centripetally by a

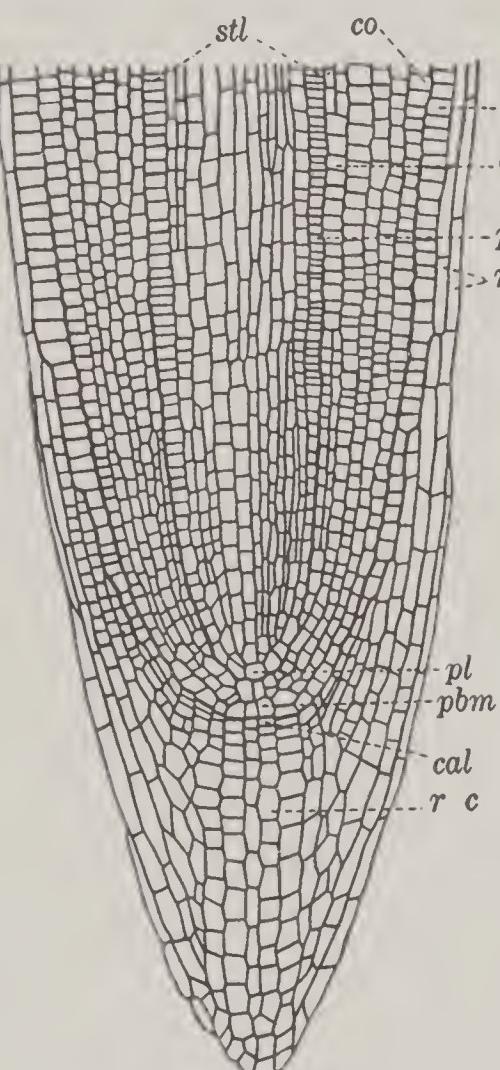
well-defined endodermis, and its outer surface is bounded by the epidermis which produces root hairs.

In the ontogeny of the root, the meristem is differentiated into three histogens. The plerome and periblem, which give rise to the stele and cortex respectively, are clearly defined; and a layer

of cells, the calyptrogen-dermatogen, overlying the periblem produces the epidermis and the root cap. (Fig. 253.) The root cap consists of several layers of cells, and those located at the tip may divide again periclinally. This differential activity results in the formation of several vertical rows of cells in the central portion of the cap so that it is thicker at its apex than at its margin. Frequently, irregularities in the orientation of the lateral cells result from these divisions and subsequent cellular enlargement.

The epidermis is produced by the final periclinal divisions of the most laterally placed cells of the calyptrogen-dermatogen layer. Each final division results in two daughter cells, the inner one becoming an epidermal initial while the outer forms a portion of the root cap. In this manner, successive cells become a part of the epidermis as the root increases in

FIG. 253. Median longisection of primary root: *cal*, calyptrogen-dermatogen; *co*, cortex; *en*, endodermis; *ep*, epidermis; *pbm*, periblem; *pcl*, pericycle; *pl*, plerome; *rc*, root cap; *stl*, stele.



This diagram illustrates a median longisection of a primary root. It shows the internal organization with various layers labeled. At the top left, labels point to the stele (stl) and cortex (co). Moving downwards, the layers are labeled on the right side: ep (epidermis), en (endodermis), pcl (pericycle), rc (root cap), pl (plerome), pbm (periblem), cal (calyptrogen-dermatogen), and rc (root cap). The diagram depicts the transition from the central stele through the periblem and cortex to the outer epidermis and root cap, illustrating the developmental sequence described in the text.

The cortex is derived from the periblem, which consists of two layers of cells overlying the plerome. The outer layer of this histogen divides only anticlinally and forms the peripheral layer of the cortex, while the inner layer divides in all planes to form the remainder of this region, which is six to nine cells in thickness at maturity. The stele is differentiated from a group of plerome cells lying above the periblem. The lateral members of this group produce the pericycle, which can be distinguished from the other regions of the stele early in ontogeny since the cells composing it are radially rather than vertically elongated. (Fig. 253.) In the development of the vascular portion of the stele, the primary

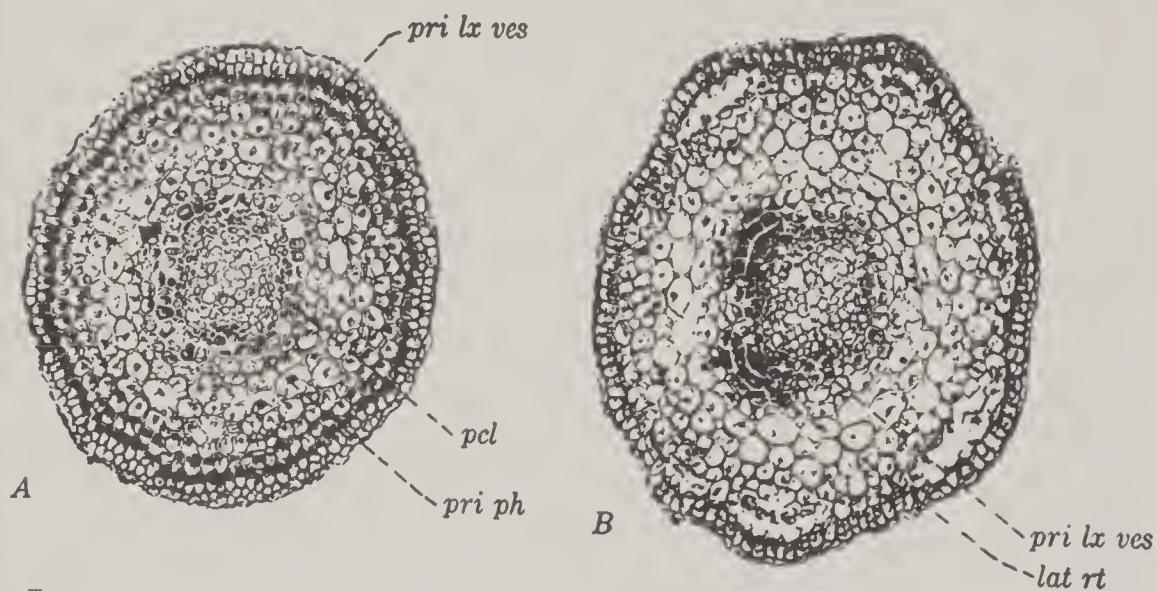


FIG. 254. *A*, transection of young primary root in region of differentiation; *B*, primary root showing origin of lateral root: *lat rt*, lateral root; *pcl*, pericycle; *pri lx ves*, primary latex vessel; *pri ph*, primary phloem.

phloem is first differentiated and four groups of elongated phloem elements are formed by longitudinal divisions of plerome cells abutting the pericycle. At the same time, a primary latex vessel is differentiated adjacent to the pericycle by the enlargement of a single vertical row of cells in each phloem group. (Fig. 254, *A*.) The cells of these vessels retain their end walls and protoplasts. The remainder of the primary phloem consists of long, very slender sieve tubes with transverse or occasionally oblique sieve plates and companion cells.

The primary xylem differentiates centripetally and the first protoxylem cells to mature are thin-walled with annular or annular-spiral thickenings. While the protoxylem elements are developing, a vertical row of parenchymatous cells at the center of the

stele becomes much enlarged and forms a single metaxylem vessel which may be separated from the adjacent metaxylem and the protoxylem points by a zone of fundamental parenchyma. In some instances, two central metaxylem vessels are formed, one of which is usually larger than the other. The outermost metaxylem elements have loosely reticulate secondary wall thickenings, while the walls of the centrally located vessel are closely reticulate.

Lateral roots are formed very early in the ontogeny of the primary root; and, before the protoxylem is completely differentiated, the development of laterals may be initiated from the cells of the pericycle lying directly outside the xylem points. (Fig. 254, B.) Tangential and radial divisions of the pericyclic cells result in the formation of a conical growing point of meristematic cells, and the subsequent development of the lateral root is similar to that described for the primary root. The laterals are usually tetrarch, occasionally triarch. Pentarch, hexarch, and other types that occur in adventitious roots were not observed in the seedling material investigated.

SECONDARY THICKENING OF THE ROOT. — The lateral or adventitious roots, which are destined to become fleshy, resemble the primary root in the organization of their primary tissues except that they are frequently pentarch or hexarch rather than tetrarch. Likewise, the ontogeny of the fleshy root, up to the time of maturation of the primary tissues, parallels that of the primary axis. There is no question but that the development of the primary xylem is exarch and that the arrangement of the primary xylem and phloem is radial, so that it is inaccurate to interpret the fleshy axis as a stem. Artschwager (1), in commenting upon this point, states that

"the validity of this assumption . . . becomes untenable when young material is studied. The exarch position of the protoxylem decides, without further argument, in favor of the root-structure theory of these organs."

At about the time that the primary xylem strand reaches maturity, the parenchymatous zone separating the primary xylem and phloem gives rise to a cambium which is irregular in outline. The first-formed secondary elements, arising from this primary cambium, are laid down in the angles between the primary xylem points and centrad to the primary phloem groups. As these angles are occupied by maturing secondary xylem elements, the

lateral extension of the cambium from the points of initial activity ultimately involves the pericyclic cells which lie outside the primary xylem points. This results in the formation of a complete cambial cylinder which becomes more and more regular in outline until it is finally symmetrical.

The relation of the activity of the centrally located parenchyma to the differentiation of the primary xylem elements has been differently interpreted by McCormick (10) and Artschwager (1). The former states that "in the young root there is usually a solid arrangement of vessels with no thin-walled parenchyma between them"; and when a root starts to thicken, parenchyma increases in amount and separates the protoxylem points from the centrally located metaxylem until each primary xylem point consists of a separate strand of one to several vessels. Artschwager, on the other hand, finds that parenchymatous activity "always precedes the differentiation of xylem on the inner face of the protoxylem groups." The activity of the primary cambium and the consequent enlargement of the axis results in a tangential stretching of the endodermal cells, and the parenchymatous cells of the cortex increase in number for a time, keeping pace with the growth of the root. Later, the intercellular spaces become larger, the tissue of the cortex disintegrates, and the epidermal cells are ruptured. (Fig. 255.)

TERTIARY THICKENING OF THE ROOT. — Up to this point, the development of the axis follows the usual sequence found in fleshy roots which thicken secondarily; but at this time, certain anomalous developments occur which complicate an interpretation of the ontogeny unless successive stages are considered in order. The first of these is the formation of secondary cambiums which originate in the parenchyma of the central portion of the axis surrounding each of the protoxylem points. (Fig. 256.) This is followed by the origin of additional secondary cambiums which may develop extensively throughout the central parenchymatous zone of the axis. These cambiums frequently occur as cylinders which surround groups of secondary xylem elements that have matured centrad to the primary cambium. (Fig. 256.) Coincident with the formation of the secondary cambiums, an active meristematic zone forms around the central metaxylem vessel, and this may increase in width until a region of considerable size is formed.

Somewhat later, secondary cambiums may arise in the tissue on the inner face of the secondary xylem which remains active for a limited period. (Fig. 257.) Still later, secondary cambiums may be formed in the parenchyma of the root which are not related spatially to any vascular elements; and these, in turn, may produce xylem centripetally and phloem centrifugally. (Fig. 258.)

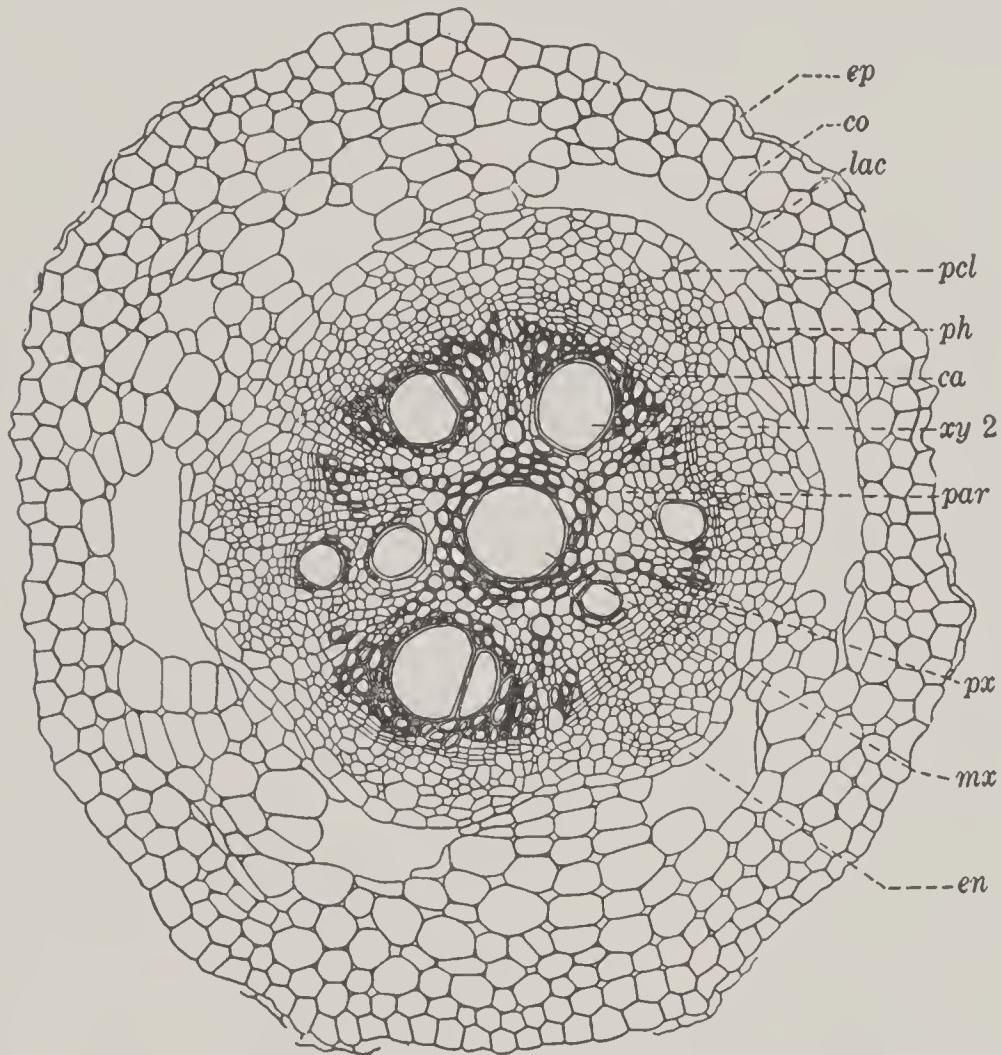


FIG. 255. Transection of young fleshy root: *ca*, cambium; *co*, cortex; *en*, endodermis; *ep*, epidermis; *lac*, lacuna; *mx*, metaxylem; *par*, interstitial parenchyma; *pcl*, pericycle; *ph*, phloem; *px*, protoxylem; *xy 2*, secondary xylem.

Less frequently, secondary cambiums may develop in the parenchyma of the original phloem groups.

While the development of these anomalous secondary cambiums is taking place, the primary cambium continues to function, forming secondary xylem and phloem elements and a large amount of storage parenchyma. The parenchyma around the secondary xylem elements may in turn produce a secondary cambium which forms new elements in the usual manner, and Artschwager (1)

reports that "when the amount of tissue produced by the secondary cambium is considerable, as can best be seen in the region of the large central cell of the young root, a tertiary cambium develops

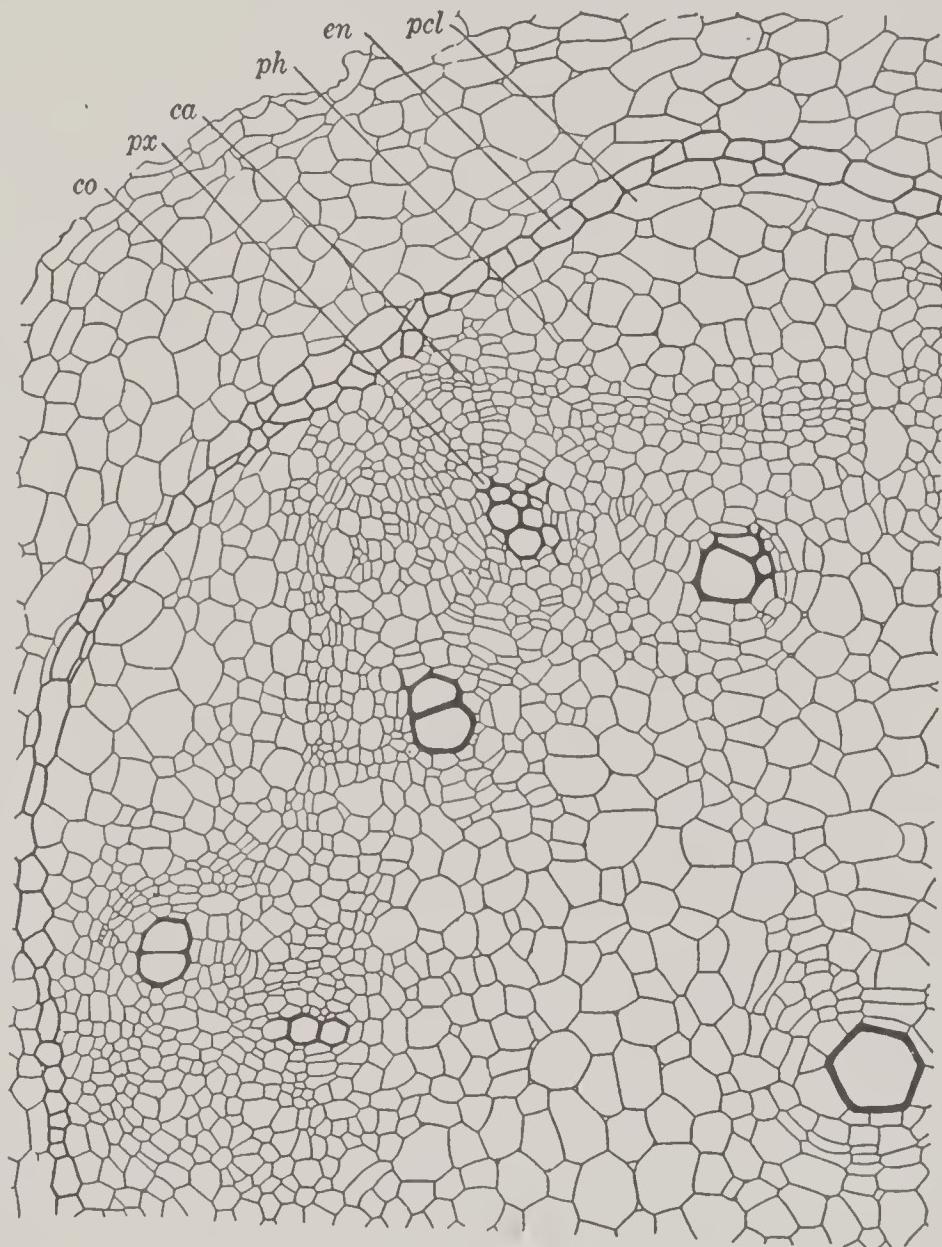


FIG. 256. Transection of portion of young fleshy root showing origin of cambium. A secondary cambium is being initiated around large metaxylem vessel at lower right-hand corner of figure: *ca*, primary cambium; *co*, cortex; *en*, endodermis; *pcl*, pericycle; *ph*, phloem; *px*, protoxylem. (After Artschwager, *Jour. Agr. Res.*)

around a number of the secondary elements and increases in the same way as did the group from which it arose."

In roots which become ridged at maturity, the lobes are traversed by vascular bundles which originate in the primary vascular ring and are diverged into the cortex, continuing vertically through the ridges. (Fig. 259.) Small bundles are occasionally present in the

peripheral portion of the cortex even in types where the ridges are lacking.

As the development of the axis proceeds, the endodermis and cortical parenchyma fail to keep pace with the growth of the stele, although there is evidence of some anticlinal division of the epidermal cells which become very much stretched tangentially. An ephemeral periderm may originate in the cortical cells, but they soon disintegrate; and, as this occurs, a phellogen is formed in the pericycle which produces the periderm of the mature root.

THE MATURE FLESHY ROOT. — In the mature fleshy root, the epidermis, cortical parenchyma, and endodermis are no longer

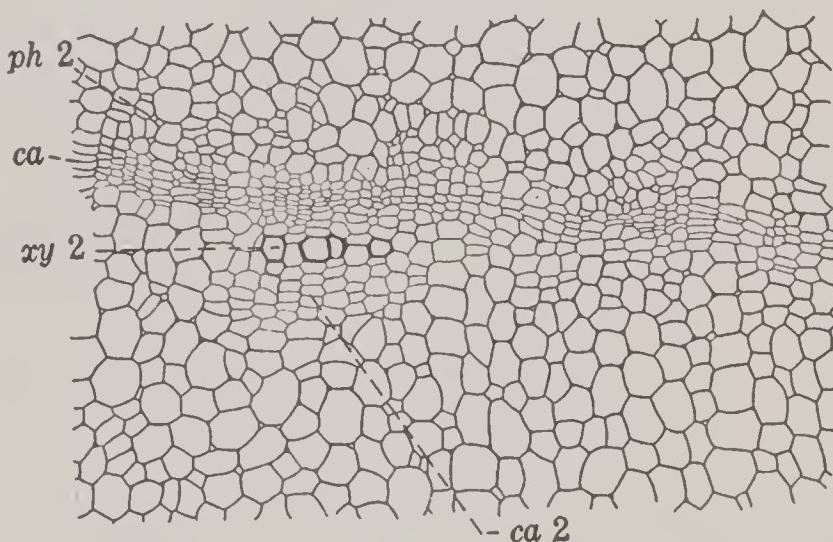


FIG. 257. Transection of portion of cambial zone of larger fleshy root showing formation of secondary cambium inside of group of secondary xylem elements: *ca*, cambium; *ca* 2, secondary cambium; *ph* 2, secondary phloem; *xy* 2, secondary xylem. (After Artschwager, *Jour. Agr. Res.*)

present and the protective "skin" consists of a pericyclic periderm which has been maintained by an active phellogen throughout the period of its growth and enlargement. Within the periderm, the pericyclic zone is composed of large parenchymatous cells which are filled with starch, and these abut projecting zones of phloem consisting of radial rows of sieve tubes and companion cells which are somewhat irregularly arranged because of the anomalous method of axial growth. The large secondary sieve tubes have transverse sieve plates, and in some regions two or three large lateral sieve fields may be formed. The companion cells are smaller in diameter than the sieve tubes but equal them in length.

The cambium also produces vertical rows of lactiferous cells which form the latex vessels. The cells retain their transverse

walls and differ in this respect from plants having a latex system in which a continuous tube is formed by the resorption of the end walls. (Fig. 260.) The prominent latex vessels may be recognized in young tissue by their large size and by their white viscid contents in which oil droplets are in suspension; but in older tissue, they are less readily identified owing to the increased size of the adjacent cells. The elements of the secondary xylem consist of both wide and narrow vessels in which the vessel segments are interconnected by a single large pore. The walls are pitted and tyloses frequently develop in the larger vessels.

Artschwager (1) classifies the storage parenchyma under two types:

"(a) normal bundle parenchyma which, like the xylem and the phloem, is a product of the cambium; (b) interstitial parenchyma — a filler between the groups of bundles. The interstitial parenchyma can be considered the direct progeny of the

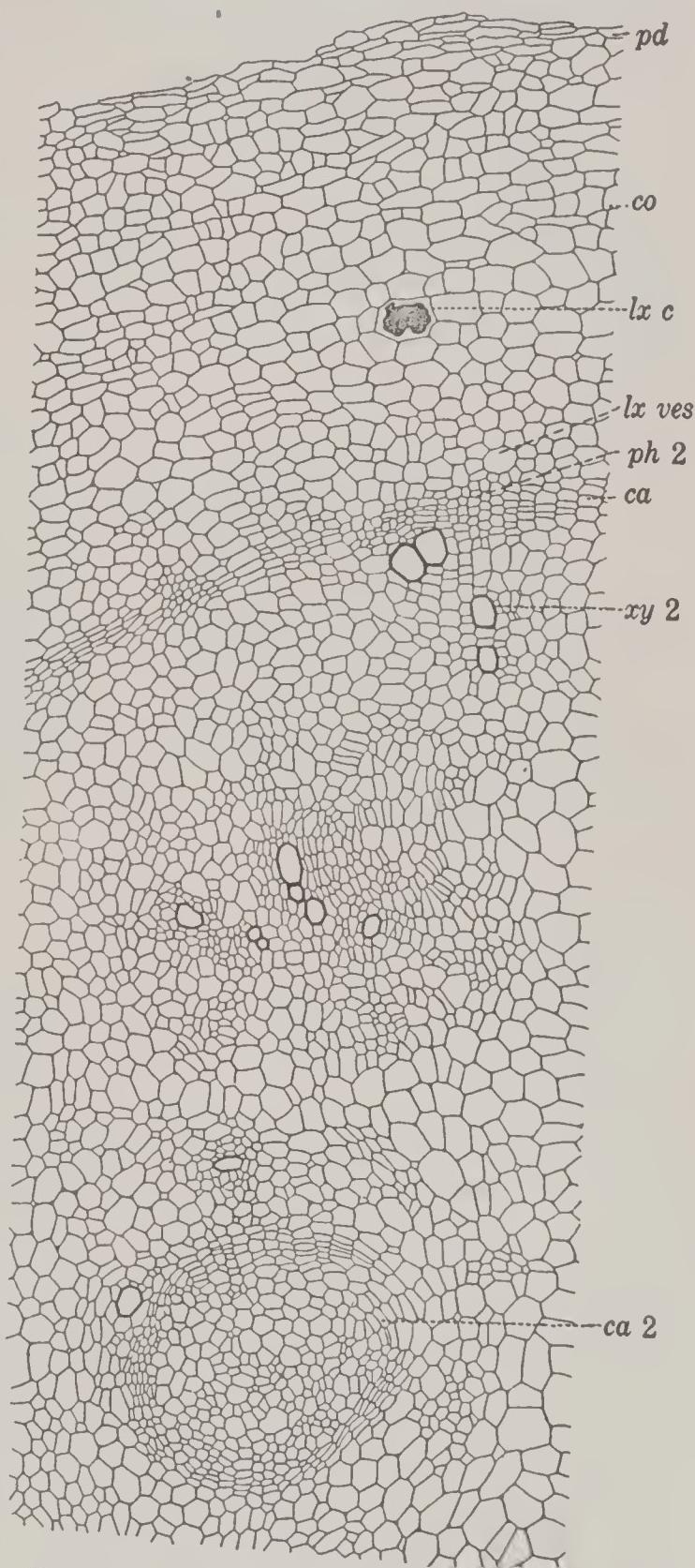


FIG. 258. Transection of portion of fleshy root about 10 mm. in diameter: *ca*, cambium; *ca* 2, secondary cambium; *co*, cortex; *lx c*, latex cell; *lx ves*, latex vessel; *pd*, periderm; *ph 2*, secondary phloem; *xy 2*, secondary xylem. (After Artschwager, *Jour. Agr. Res.*)

cells of the parenchymatous sheath of the young rootlet. It forms irregular areas and even broad zones, which are distinguishable from the surrounding tissue by their lighter color. The cells composing it are commonly irregular, elongated, and poor in starch. The cells of the bundle parenchyma are polyhedral and fairly uniform; they are very rich in starch and possess a well-developed nucleus."

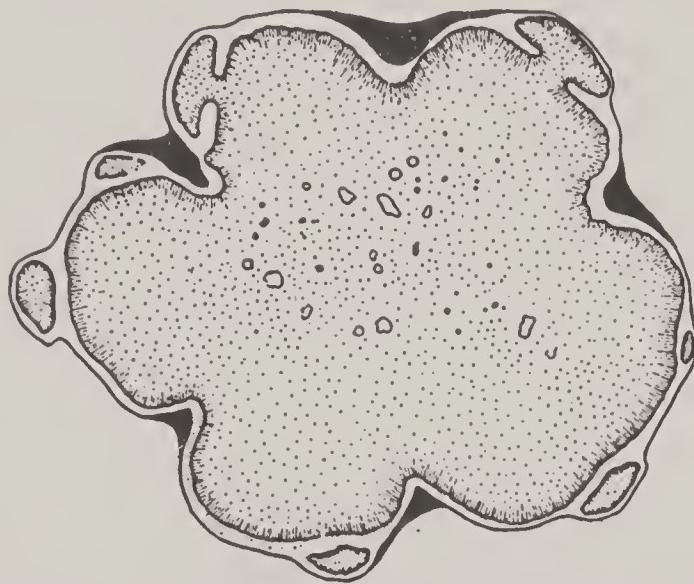


FIG. 259. Diagrammatic transection of mature fleshy root. (After Artschwager, *Jour. Agr. Res.*)

phloem are alternate and radial but the central portion of the stele is parenchymatous. At successively higher levels, near the middle of the hypocotyl, there is a gradual re-orientation of the primary vascular tissue. The four phloem regions are divided into wide arcs consisting of scattered groups of phloem cells which lie immediately inside the pericycle and alternate with the primary xylem points. The metaxylem elements differentiate in a tangential position with respect to the protoxylem so that each of the four xylem poles consists of the protoxylem point with two tangential arms of metaxylem. (Fig. 261, A.)

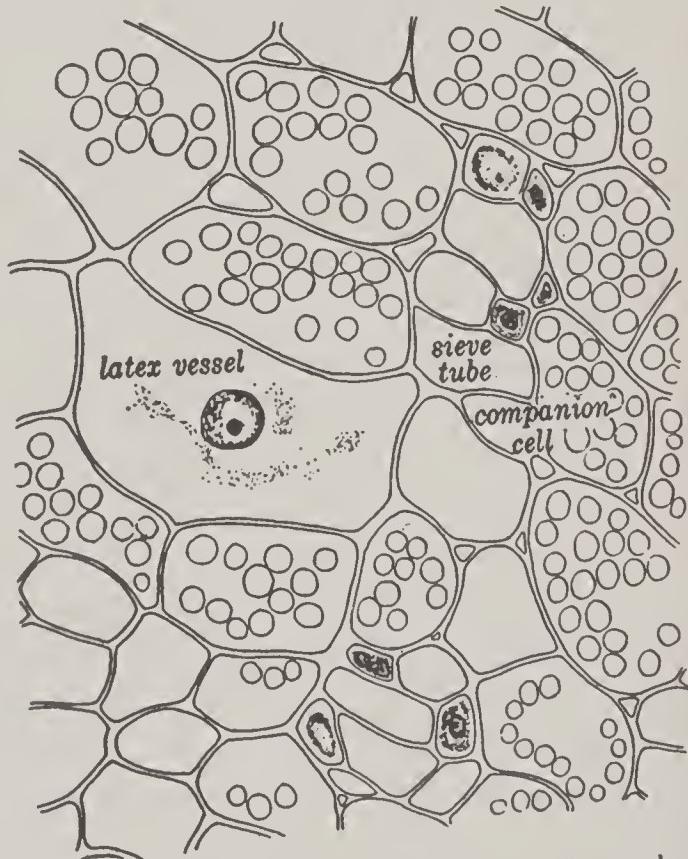


FIG. 260. Transection of radial row of secondary sieve tubes with companion cells and adjacent latex vessel. (After Artschwager, *Jour. Agr. Res.*)

In the upper hypocotyl, the four arcs of scattered phloem groups are extended tangentially so as to form a discontinuous ring of phloem elements some of which are collateral with the metaxylem. The first strands of inner phloem are differentiated in the pith and lie between the two laterally divergent arms of the metaxylem of each xylem pole. (Fig. 261, B.) The inner phloem is not continuous with the primary phloem of the root, and arises later in ontogeny than the outer phloem of the hypocotyl which is continuous with that of the root. It consists of strands that have

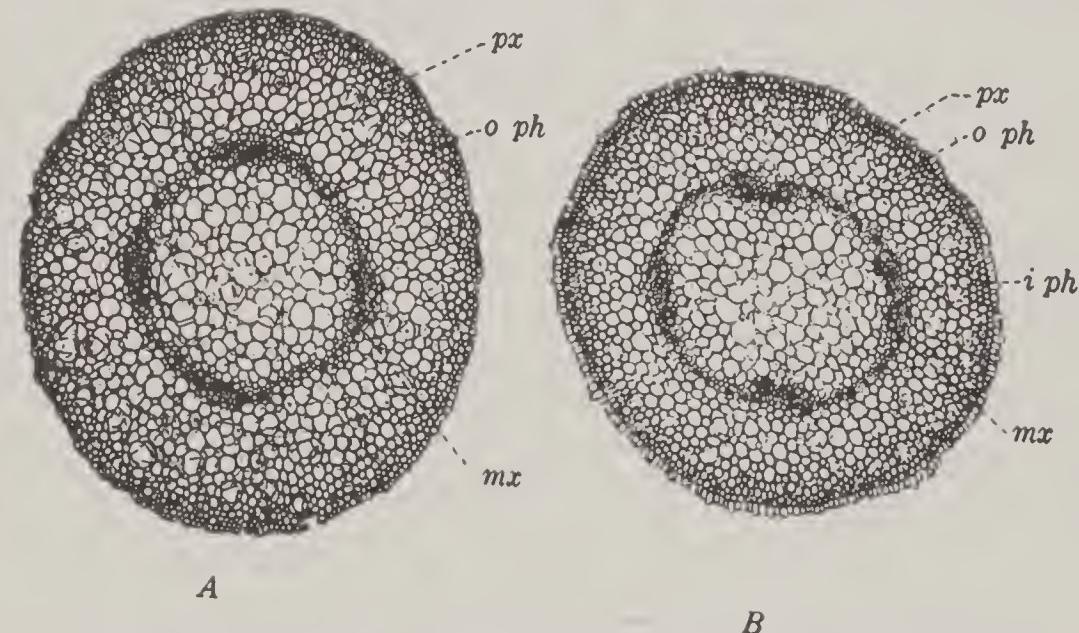


FIG. 261. *A*, transection of lower portion of hypocotyl of three-weeks-old seedling showing tangentially oriented metaxylem arms; *B*, transection through upper portion of same showing further divisions of metaxylem and appearance of inner phloem: *i ph*, inner phloem; *mx*, metaxylem; *o ph*, outer phloem; *px*, protoxylem.

differentiated downward from the cotyledonary plate as continuations of the inner phloem of the bicollateral bundles of the cotyledonary traces.

There is usually no connection between the outer and inner phloem, and the strands of the latter end blindly in the pith of the hypocotyl. In the case illustrated in Figure 262, no interconnection between the outer and inner phloem occurred above or below the level figured; but, in a few instances, they may be transversely connected by the differentiation of parenchymatous cells lying in the gap between the divergent and partially separated arms of the primary xylem. The relationship of the inner phloem to the outer has been variously interpreted by investigators who have worked with other members of this family. Scott (11), in his investigation of *Ipomoea versicolor* Meissn., states that

"the internal phloem extends downwards into the hypocotyl and passes out between the converging protoxylem groups of each cotyledonary pair of bundles, thus joining the external phloem of the root."

In his summary, he concludes that

"As regards the course of the internal phloem in the transition from stem to root, *Ipomoea versicolor* may be taken as typical of plants with bicollateral bundles generally."

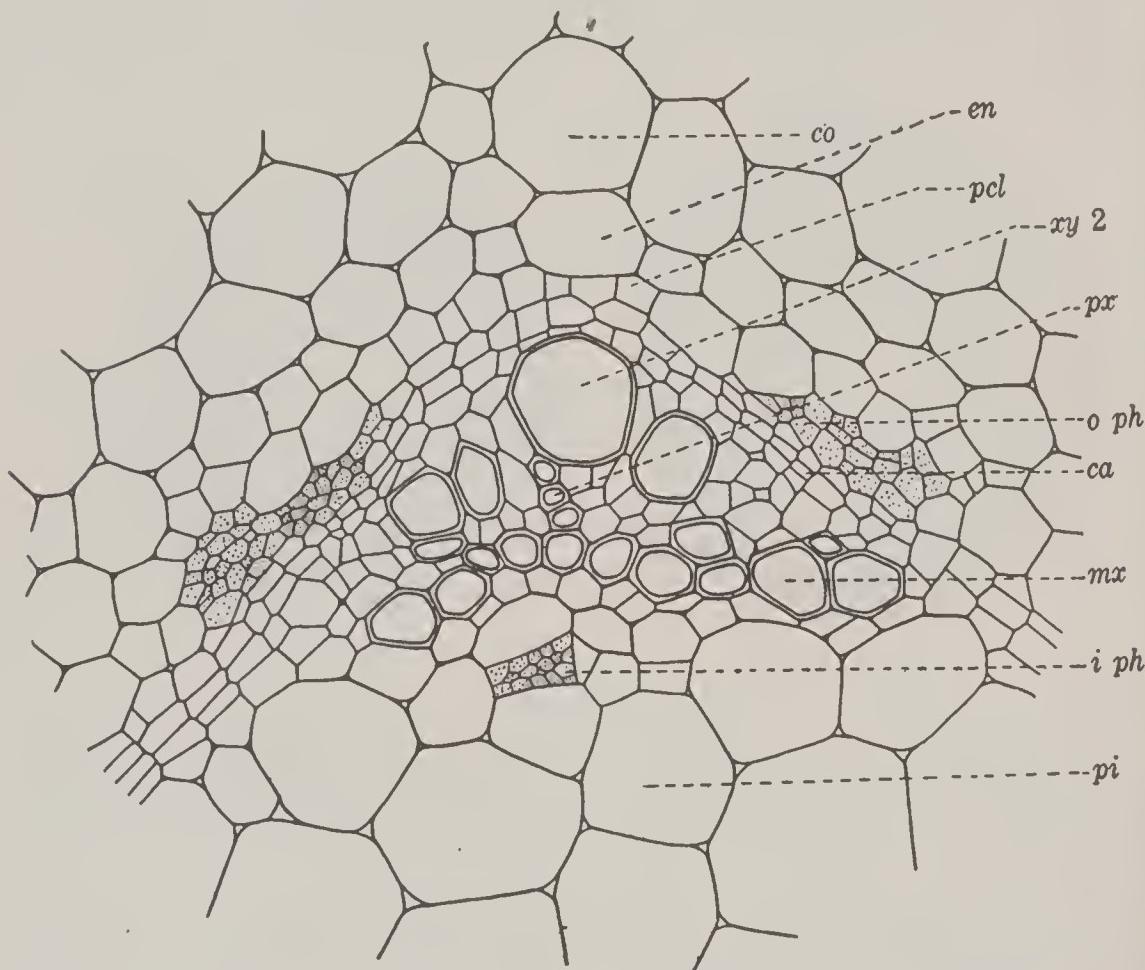


FIG. 262. A protoxylem point in lower hypocotyl of three-weeks-old seedling: *ca*, cambium; *co*, cortex; *en*, endodermis; *i ph*, inner phloem; *mx*, metaxylem; *o ph*, outer phloem; *pcl*, pericycle; *pi*, pith; *px*, protoxylem; *xy 2*, secondary xylem.

Lee (8) investigated the seedling anatomy of *Convolvulus tricolor* L., var. major, and also *C. tricolor* L. In regard to the former he concludes that

"The phloem is extremely small in amount and at no point can internal phloem be recognized with certainty — an observation which emphasizes the late appearance of this tissue noticed by other observers."

In *Convolvulus tricolor*, he notes frequent anastomoses of strands of phloem connecting the bundles in the petiole of the cotyledon, and

also calls attention to the abundance of inner phloem in the petiole and hypocotyl. In this instance, he agrees with Scott, stating that

"in the upper part of the hypocotyl, during the rearrangements in the cotyledonary strand so that the protoxylem becomes external, the internal phloem masses of that bundle fuse, and the fused mass gradually passes out between the metaxylem groups (before the latter meet to form the root bundles) and joins on to the external phloem. The same events take place at a lower level in connexion with the intercotyledonary bundles, so that finally an ordinary tetrarch root is produced."

Lamounette (7) investigated several of the Convolvulaceae, including *Ipomoea leucantha*, and concluded that the inner phloem, when present in the hypocotyl, is differentiated in the medullary parenchyma and is not continuous with the outer phloem of the root. In fact, he rejects the term *bicollateral*, supporting Héral (4) in this regard.

In the sweet potato, anastomoses between inner and outer phloem occur at the base of the cotyledonary petiole, but there is no evidence to indicate that the inner phloem of the hypocotyl is regularly connected with the outer phloem. The inner phloem may be regarded as supplementary to the outer, and its appearance late in the ontogeny of the seedling, at a time when it is beginning to function photosynthetically, suggests a correlation between the function of the phloem and its anatomical development.

In the upper hypocotyl, the cotyledonary plane may be distinguished from the intercotyledonary by the degree of separation of the two metaxylem groups in each case. Slightly below the cotyledonary node, the metaxylem groups of each intercotyledonary strand are more widely separated from each other than those of the cotyledonary strand, each group inclining toward one of the latter. At this level, the inner phloem is well developed, so that there are two bicollateral polar bundles of the double bundle type, and four smaller laterally placed bicollateral bundles derived from the intercotyledonary strands.

At the cotyledonary node, the two lateral bundles of each cotyledonary trace abut the right and left flanks of the median double bundle of the trace so that it appears to be a single large crescentic unit. Slightly above the level of divergence of the cotyledonary traces from the vascular ring, the lateral bundles of each trace separate from the median bundle which is itself divided to form

two b collateral bundles. The xylem of the median bundle is not endarch in its development, but consists of a single protoxylem strand and two tangentially oriented metaxylem groups which lie between the outer and inner phloem.

THE COTYLEDONS. — The slender cotyledonary petiole equals or slightly exceeds the lamina in length, and its adaxial surface is grooved so that it is crescentic in transection. There are four bundles at its base; and in the two large median b collateral bundles, the outer phloem consists of several scattered groups of cells while the inner phloem is composed of two or three strands. In some instances, the xylem may be surrounded by a discontinuous ring of phloem elements so that the bundle is essentially amphicribral.

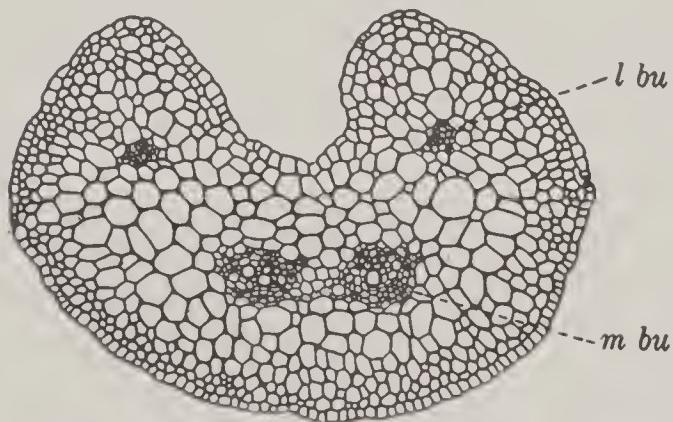


FIG. 263. Transection of cotyledonary petiole:
l bu, lateral bundle; m bu, median bundle.

The two smaller lateral bundles are collateral or half-amphicribral. (Fig. 263.) The parenchymatous cells surrounding the bundles are thin-walled with large intercellular spaces. Toward the abaxial surface, the outer cell layers are compact and collenchymatous but contain chloroplasts.

The subepidermal cells of the adaxial surface are also chlorophyllose, but not so compactly arranged, and the more numerous stomata open into large intercellular spaces.

The arrangement of the petiolar bundles remains unchanged up to a point slightly below the lamina, where the two median bundles anastomose to form a single broad one. (Fig. 264, A.) At the base of the lamina, the two small bundles (a, a') curve abruptly outward and supply the auricles. The median bundle cuts off two lateral branches (b, b') which immediately give rise to two small laterals (c, c') that supply the basal portion of the lamina. The median bundle finally forks just below the notch of the blade, one branch extending into each lobe (d, d'), and these with the branches (b, b'), supply the lobes of the cotyledon.

The median bundle is still b collateral at the base of the lamina, but the inner (adaxial) phloem ends blindly in the mesophyll before the strand forks. The other veins are collateral throughout their

extent in the blade, and there is a progressive reduction in the amount of phloem tissue in succeeding branches until the ultimate veinlets consist of a single spiral tracheid.

The primary xylem, which is tangentially oriented in the petiole, is differentiated in a manner equivalent to the endarch condition in stems with the protoxylem elements toward the upper surface of the cotyledon.

The cells of the upper epidermis of the lamina are larger than those of the lower, irregular in size, and their outer walls are somewhat convex so that the surface is roughened. Stomata occur in

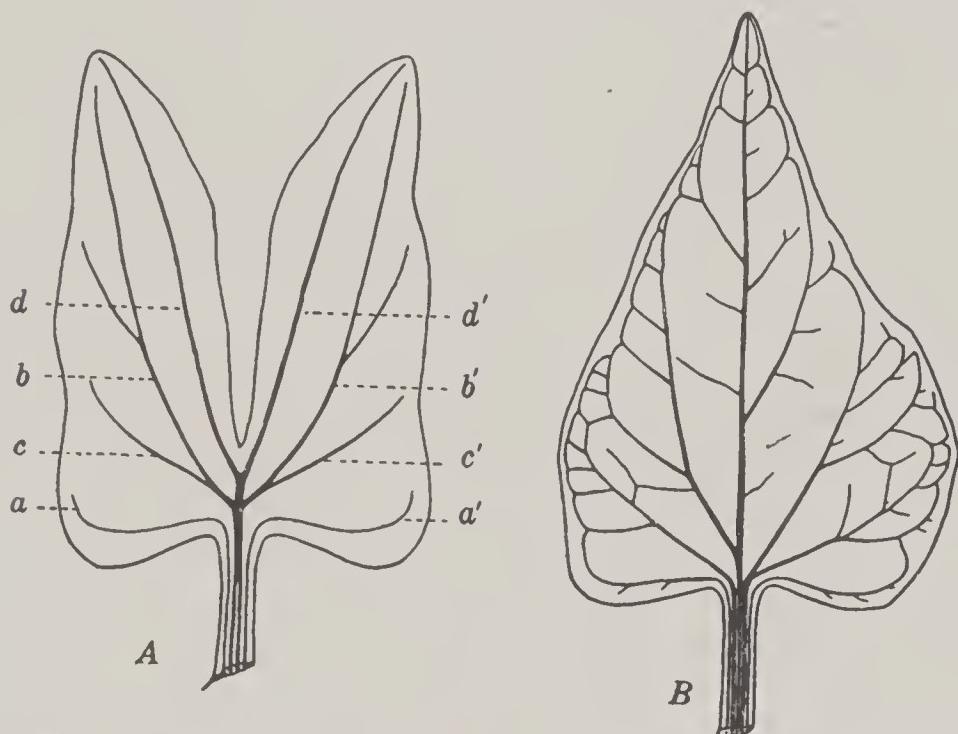


FIG. 264. A, outline drawing of mature cotyledon showing venation of lamina and petiole; B, same of foliage leaf.

both epidermal layers but are more abundant in the lower one. In the mesophyll, the palisade parenchyma is loosely organized, and usually consists of two rows of cells, but interspersed with them are cells whose length equals that of the double palisade. The spongy tissue is four or five cells in thickness, except at points where the principal veins traverse it; and the isodiametric cells are so arranged that large lacunae and substomatal cavities are formed. In the region of the principal veins, the mesophyll is more compact and the palisade tissue and spongy cells are replaced by collenchymatous cells above and below the vein. (Fig. 265.) Glandular scales or hairs occur on the lower epidermis and each consists of a basal cell subtending several elongated ones that are

arranged in a disk to form the flattened or convex surface of the scale.

THE ANATOMY OF THE YOUNG STEM. — The epidermis of the young stem is thin-walled and produces numerous glandular scales and non-glandular hairs. The scale has a flat basal cell which arises from a small somewhat sunken epidermal cell so that the terminal portion of the scale appears to rest in a saucer-like depression in the epidermal surface. (Fig. 266, A.) The distal part is composed of several cells which are formed by vertical divisions of

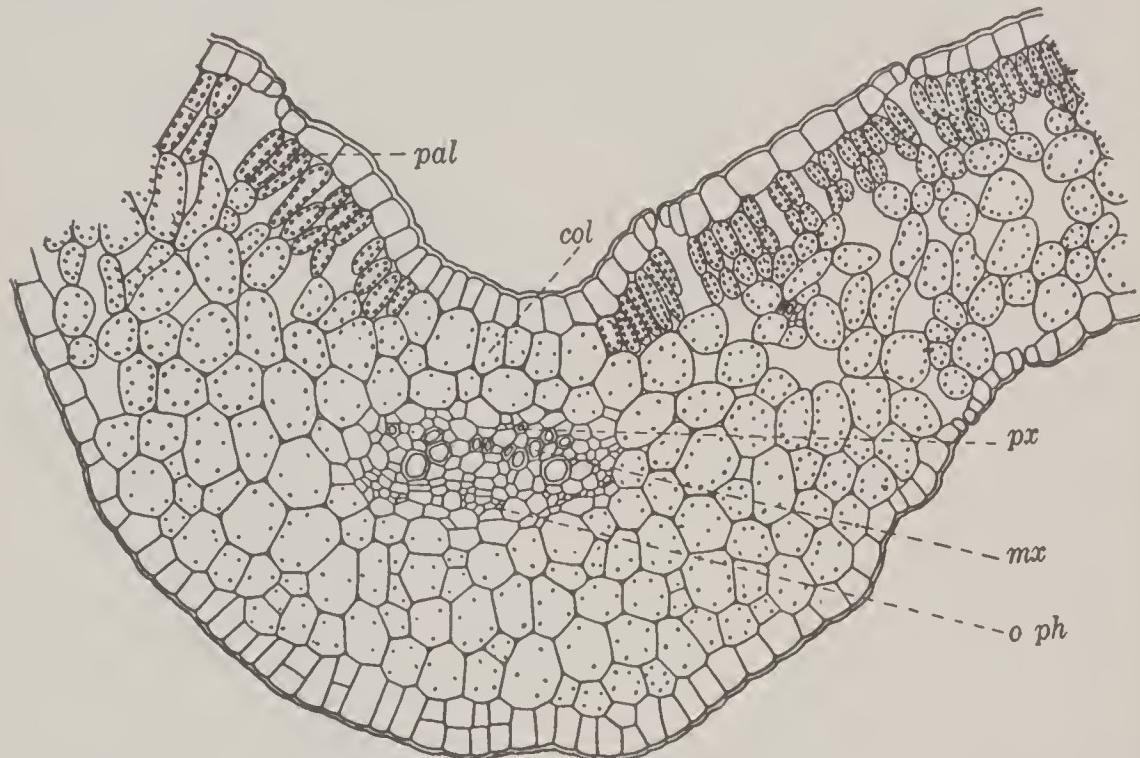


FIG. 265. Transection of portion of lamina of cotyledon through midvein: *col*, collenchyma; *mx*, metaxylem; *o ph*, outer phloem; *pal*, palisade; *px*, protoxylem.

the terminal cell of the scale. The non-glandular hair has a basal stalk cell which arises from an epidermal cell or a group of epidermal cells and a tubular terminal portion which is divided transversely into two or more cells. (Fig. 266, B.) These hairs may or may not persist on the mature stem, and their frequency appears to be a varietal character. The stoma is somewhat raised above the adjacent epidermal cells, due in part to the position of the two accessory cells which lie parallel to the guard cells. (Fig. 266, C.)

The cortical chlorenchyma is compact and there are numerous vertical latex canals, usually bounded by four to six secreting cells, located centrad to the two hypodermal layers. Crystals of calcium

oxalate are abundant in the parenchymatous cells of both the cortex and pith. The endodermal cells are distinct and can be recognized by the relative density of their cell contents. Within the endodermis, there are two or three layers of pericyclic cells and abutting these are small scattered groups of outer phloem consisting of narrow thin-walled elements.

Early in ontogeny, the procambial ring is well defined so that it forms a continuous cylinder in the young stem. The vessels of the primary xylem are spiral or variously reticulated. The inner phloem, like the outer, is comprised of isolated groups of sieve tubes and companion cells which are much smaller in diameter than the adjacent parenchyma of the pith. They are not always in radial alignment with the primary xylem; and, for this reason, do not exhibit a strictly bicollateral arrangement such as occurs in the Cucurbitaceae. The parenchymatous cells of the pith are large with intercellular spaces, and there are numerous latex canals and crystal inclusions similar to those found in the cortex.

THE MATURE STEM. — In the mature stem, the epidermis is somewhat thick-walled and cutinized with relatively few glandular and non-glandular hairs so that the surface is usually glabrous. Lenticels are numerous and the tabular thin-walled cork cells forming them are produced by periclinal divisions of the epidermal cells adjacent to a stomatal opening or by similar divisions of the hypodermal layer. In cases where periderm formation has occurred, the cells of the hypodermis are in radial alignment with the adjacent epidermal cells. Within the hypodermal layer are several rows of compact parenchymatous or collenchymatous cells which form the outer zone of the cortex. The inner zone consists of large parenchymatous cells which undergo considerable tangential elongation and some anticlinal division to compensate for the secondary thickening of the stele. The latex canals persist but are somewhat difficult to recognize because of the increased size of the adjacent cells. The endodermis is well defined, and, in the under-

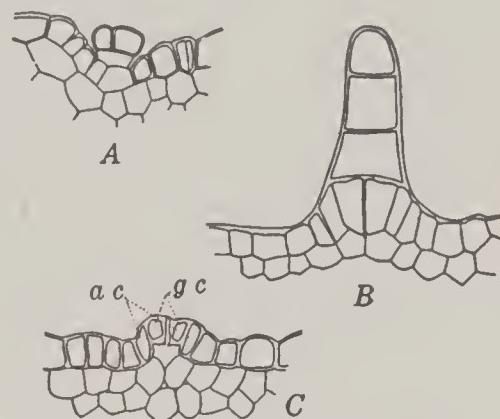


FIG. 266. A, detail of young glandular scale; B, young non-glandular epidermal hair; C, stoma with guard cells and accessory cells: ac, accessory cells; gc, guard cells.

ground portion of adventitious stems which arise from the fleshy roots, Casparyan strips are well developed.

The pericycle is one to three cells in width and a discontinuous cylinder of pericyclic fibers is differentiated in it, some of which are very much thickened. (Fig. 267.) The outer phloem, in addition to sieve tubes and companion cells, consists of parenchyma which frequently contains crystals of calcium oxalate, and a few

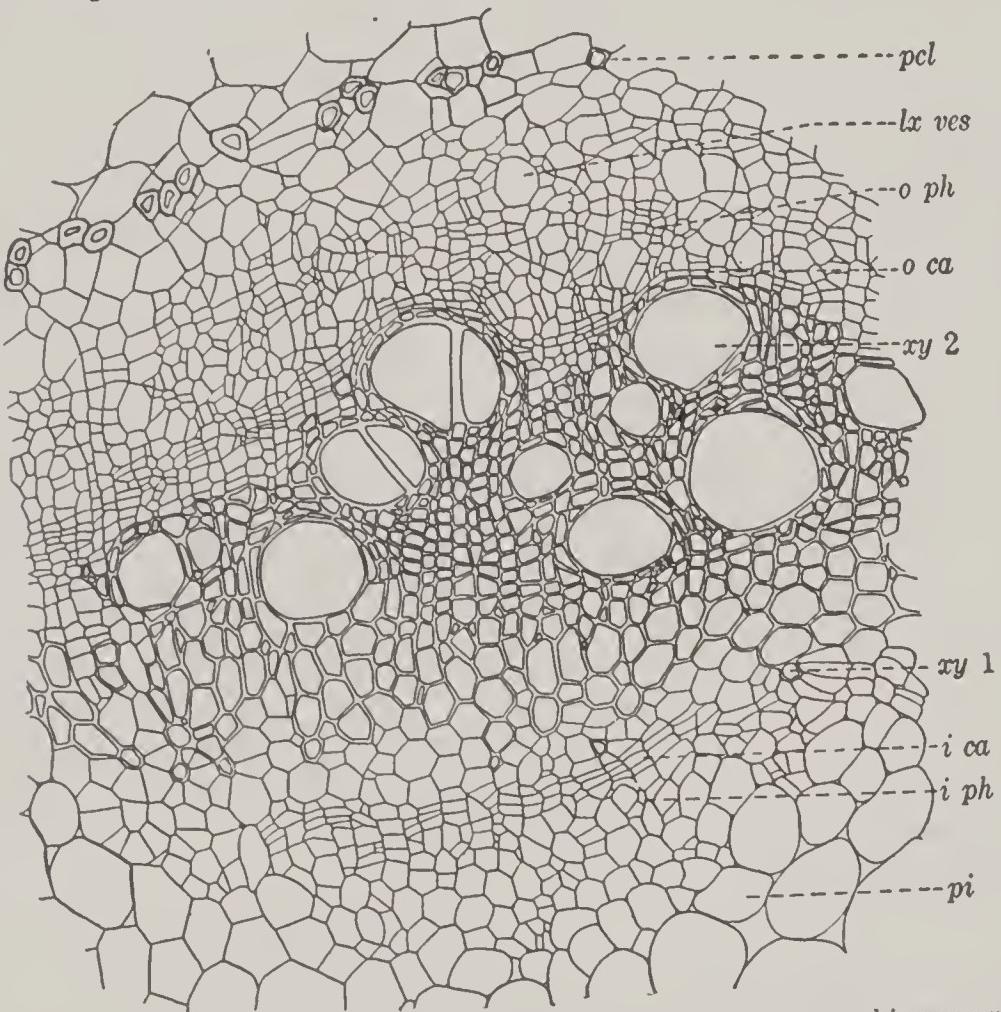


FIG. 267. Transection of sector of stele of mature stem showing outer and inner cambiums: *i ca*, inner cambium; *i ph*, inner phloem; *lx ves*, latex vessel; *o ca*, outer cambium; *o ph*, outer phloem; *pcl*, pericyclic fiber; *pi*, pith; *xy 1*, primary xylem; *xy 2*, large secondary xylem vessel.

latex canals may occur adjacent to the pericycle. The cambium forms a continuous cylinder early in ontogeny as a result of the development of an active interfascicular cambium. In the stele, there are commonly two or three bundles which have larger vessels than the intervening ones; and it is characteristic of the stem of *Ipomoea*, as well as of many other representatives of the Convolvulaceae, that these bundles are located in two groups which lie approximately opposite each other in the vascular cylinder. The

large vessels have bordered pits and are surrounded by smaller ones and by parenchyma that becomes thick-walled as the stem matures. The pits of the wood parenchyma are simple, and half-bordered ones occur where the vessels and parenchyma are adjacent to each other. The interfascicular regions are characterized by radial series of thick-walled elements, and groups two to five rows in width are separated from adjoining ones by a row of thin-walled ray-parenchyma cells.

Between the protoxylem and the inner phloem, there is a region of thin-walled parenchyma; and, in this zone, an inner cambium may arise which is relatively inactive and seldom forms a continuous inner cambial ring. It usually produces additional phloem centripetally; and, less frequently, may cut off a few secondary xylem elements centrifugally, in which case bundles with a reverse orientation are formed. The inner phloem consists of scattered groups of companion cells and sieve tubes, and the pith is as described for the young stem.

THE DEVELOPMENT OF THE FOLIAGE LEAVES. — At the time of the differentiation of the first foliage leaves, the epicotyledonary axis is surrounded by the bases of the cotyledons which form a partial sheath or cotyledonary collar. In the ontogeny of the leaf, its primordium arises from the peripheral tissues of the growing point as a conical mass of cells. The primordium elongates and broadens by general meristematic activity until it becomes somewhat crescentic or triangular in transection at the base, tapering to a rounded or slightly subtriangular apex. (Fig. 268, A.) In the basal portion of the primordium which later forms the petiole of the leaf there is an early differentiation of procambial strands. Growth in length of the primordium is accomplished by general cell division, but there is an acceleration of meristematic activity in the lateral portions of the adaxial surface. (Fig. 268, B.) This results in the formation of the lamina which develops with the upper surfaces of the two halves of the blade opposing each other. They are thus oriented at right angles to the midrib with their edges directed toward the axis of the epicotyl. (Fig. 268, C.) Following differentiation of the lamina, the petiole elongates by continued cell division and enlargement.

Glandular scales are formed in the epidermal tissue of the developing leaf. These are more numerous on the exposed lower epidermis than on the upper and resemble the scales found on the

young stem. The mesophyll is very compact at first, and there is little differentiation into spongy and palisade regions; but, later in ontogeny, the spongy tissue becomes loosely organized and large

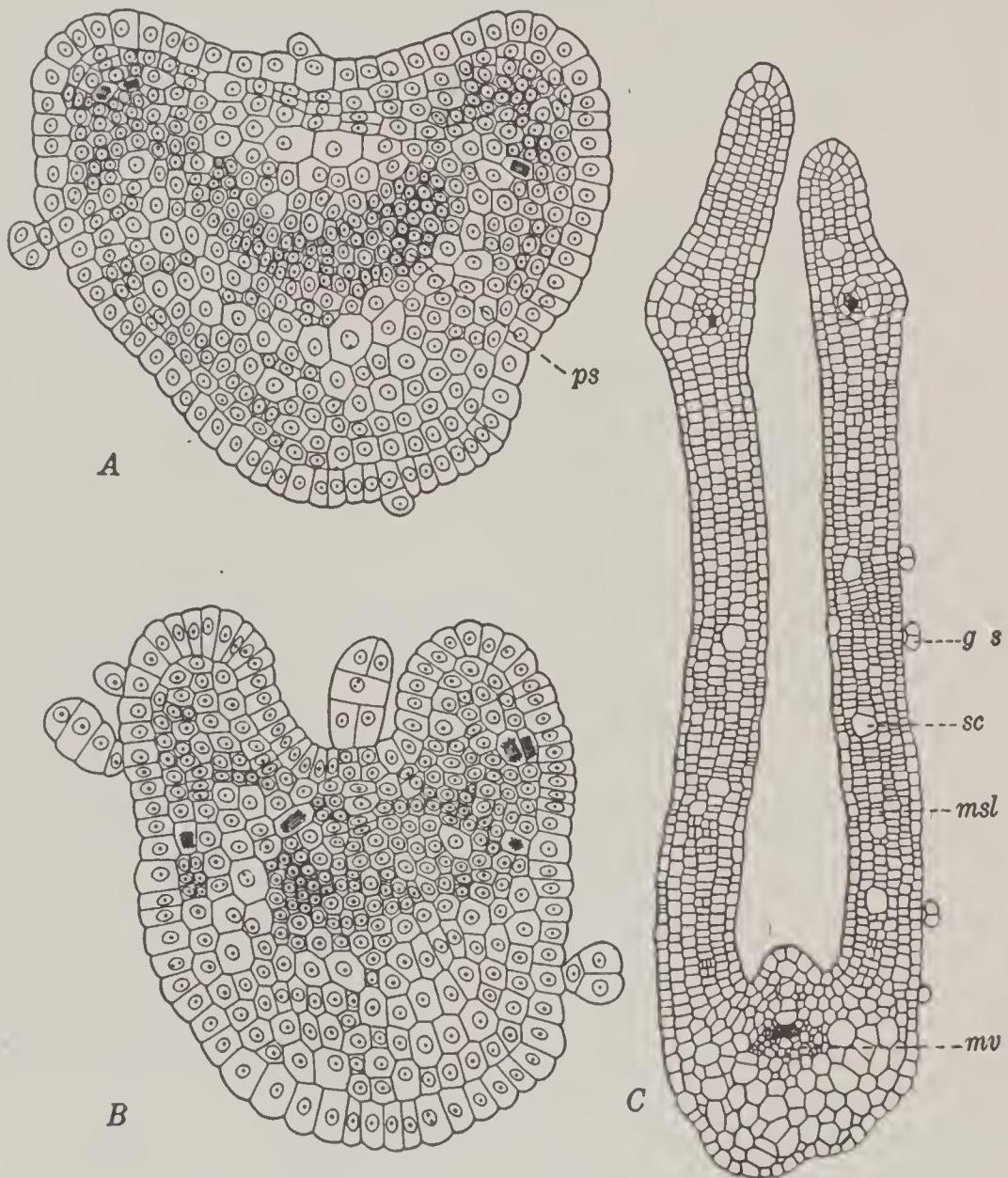


FIG. 268. Development of foliage leaf; A, transection of young leaf primordium near base showing procambial strands and region of meristematic activity; B, transection of same primordium at slightly higher level showing development of lamina; C, transection of young leaf showing orientation of lamina with respect to midvein: g.s, glandular scale; msl, mesophyll; mv, midvein; ps, procambial strand; sc, secretory cell.

intercellular spaces are formed. The palisade region consists of one to three layers of palisade parenchyma which are occasionally interrupted by groups of transversely divided parenchyma. In the young leaf, secretory cells develop between the palisade and spongy tissue, but these are less conspicuous as maturation proceeds.

THE MATURE LEAF. — At maturity, the mesophyll is much less compact and there are numerous large intercellular spaces in the spongy region and between the palisade cells. (Fig. 269.) The

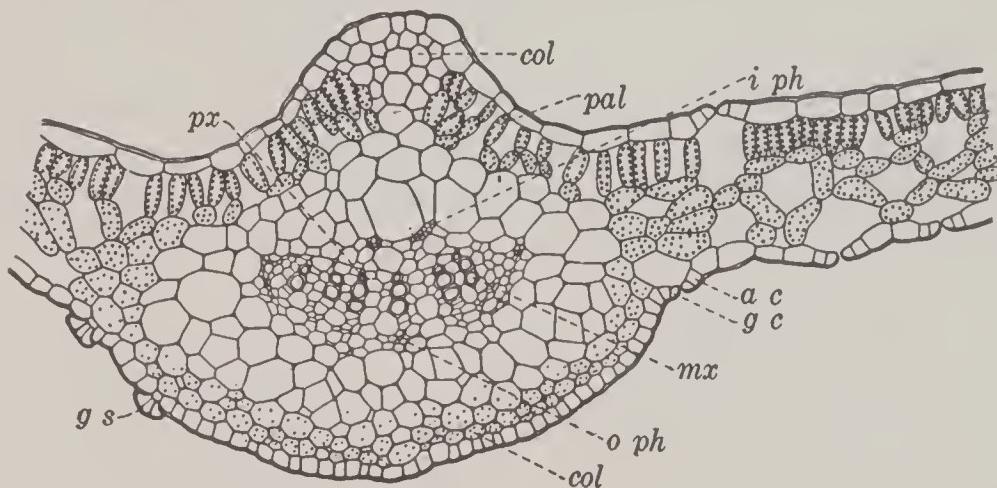


FIG. 269. Transection of base of foliage leaf through midvein: *ac*, accessory cell; *col*, collenchyma; *gc*, guard cell; *gs*, glandular scale; *i ph*, inner phloem; *mx*, metaxylem; *o ph*, outer phloem; *pal*, palisade; *px*, protoxylem.

secretory cells are not easily detected, resembling large air cavities; but, unlike intercellular spaces, they are not directly connected with adjacent air chambers owing to the retention of the original cell wall.

The epidermal cells are irregular in size and have a definite cuticle. Stomata are more numerous in the lower than in the upper epidermis and are surrounded by the guard cells and two or more accessory cells. In the development of the stoma, the epidermal initial is divided by the formation of successive walls which are oriented in such a way that several accessory cells are formed which surround the stomatal mother cell. (Fig. 270, A.) The mother cell produces the two guard cells by a final longitudinal division, and the stoma is formed by a separation of their opposed primary walls along the middle lamella. The number of accessory cells which may be formed is commonly three or four, and two of these abut the guard cells. (Fig. 270, B.)

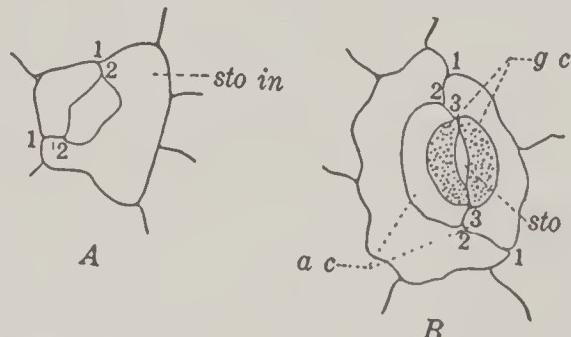


FIG. 270. *A*, early stage in stomatal formation; *B*, mature stoma with guard cells and accessory cells. Numerals 1, 1; 2, 2; 3, 3; indicate sequence of wall formation: *ac*, accessory cells; *gc*, guard cells; *sto*, stoma; *sto in*, stomatal initial.

In the region of the midrib and the principal lateral veins, the palisade is replaced by mechanical tissue above the vein which forms a protecting ridge on the adaxial surface; and a zone of collenchyma develops below the vein. The midvein is bicollateral at the base of the leaf, but there is a reduction in the amount of adaxial (inner) phloem toward its tip until finally the collateral arrangement is attained. The lateral veins are collateral; but, like the midvein, there is a reduction in the amount of phloem, in this case the abaxial (outer) phloem, and the ultimate veinlets terminate as single spiral tracheids.

At the base of the leaf, there are five principal veins which extend for some distance down the petiole without anastomosing. (Fig. 264, B.) The three median ones are bicollateral, while the two laterals are half-amphicribral or collateral. At the base of the petiole, the two lateral bundles anastomose with the right and left median bundles, so that at this point there are two large lateral bundles and a smaller median one. The leaf traces of the first, second, and third foliage leaves constitute the primary vascular tissue of the first internode, which consists of eight or nine endarch, bicollateral bundles. Near the cotyledonary plate, these converge to form two lateral zones of the stele which become confluent with the lateral bundles of the cotyledonary traces in the intercotyledonary plane.

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CHAPTER XVII

SOLANACEAE

SOLANUM TUBEROSUM

THE nightshade family, Solanaceae, contains many important vegetable crops including: potato, *Solanum tuberosum* L.; eggplant, *S. Melongena* L.; tobacco, *Nicotiana Tabacum* L.; tomato, *Lycopersicum esculentum* Mill., and several varieties of pepper belonging to the genus *Capsicum*. In addition, some members of the family are grown as ornamentals, and a number of them produce alkaloids that are used as drugs.

The potato plant is a native of the highlands of South and Central America, and a wild tuber-producing form, *Solanum Jamesii*, is still found in the mountains of Arizona, Colorado, Texas, Utah, and Mexico. The wild species resemble the cultivated *Solanum tuberosum*, except that the latter has a larger vine and a more pronounced development of tubers. Berthault (4) regards *Solanum tuberosum* as a distinct species which has not been derived from native ones by selection or mutation, and points out that it differs from the wild tuberous forms in its floral organization, especially with respect to its rotate corolla and the sharp-pointed, mucronate, calyx lobes.

GENERAL MORPHOLOGY

The potato is an annual, herbaceous dicotyledon as far as its vegetative and flowering habits are concerned, but it may be regarded as a potential perennial owing to its capacity for vegetative reproduction by means of tubers. These arise on underground stems and from them new shoots are produced.

THE STEM. — The aerial stem is herbaceous and erect in its early development, but later may become spreading and semi-prostrate. It reaches a height of 2 to 5 feet or more; and, after becoming procumbent, may produce several axillary branches. The stems are green or purplish, and are round to subtriangular or quadrangular

in transection. In some cases, the angular margins form ridges or wings which are prominent in young plants. (Fig. 271.)

THE LEAF. — The leaves are alternate with a $\frac{5}{13}$ phyllotaxy, and the spiral is usually counter-clockwise. The petioles are semicircular in transection with a convex abaxial and a slightly concave adaxial surface. The base of the petiole is flattened somewhat and ensheathes about one-third of the circumference of the stem at the node. The wing-like margins of the petiole are unequally decurrent, one extending down the stem through a single internode, the other through two. In plants grown from seed, the first leaves above the cotyledons are simple, and this may be the case with the first leaves arising on stems grown from tubers. (Fig. 272.) The later leaves are compound and irregularly odd-pinnate with more or less petioled leaflets.

The number of leaflets varies considerably with the variety, and, in addition to the terminal one, there are usually three or four pairs of large, oval leaflets with entire or serrate margins. Smaller, secondary leaflets sometimes occur between the large primary ones. The young leaflets are densely pubescent, bearing hairs of several types, some of which are long and straight consisting of one to several cells, while others are short and glandular with a spherical head of four cells which is borne upon a short slender stalk cell. At maturity, the leaf is sparingly pubescent, the persistent hairs occurring chiefly along the midrib and lateral veins.

The leaflets are net-veined; and branches arise from the prominent midrib, forming a dense reticulate system. The lateral veins extend toward the apex and margins of the leaf, anastomosing freely so that the marginal portions have a greater compactness

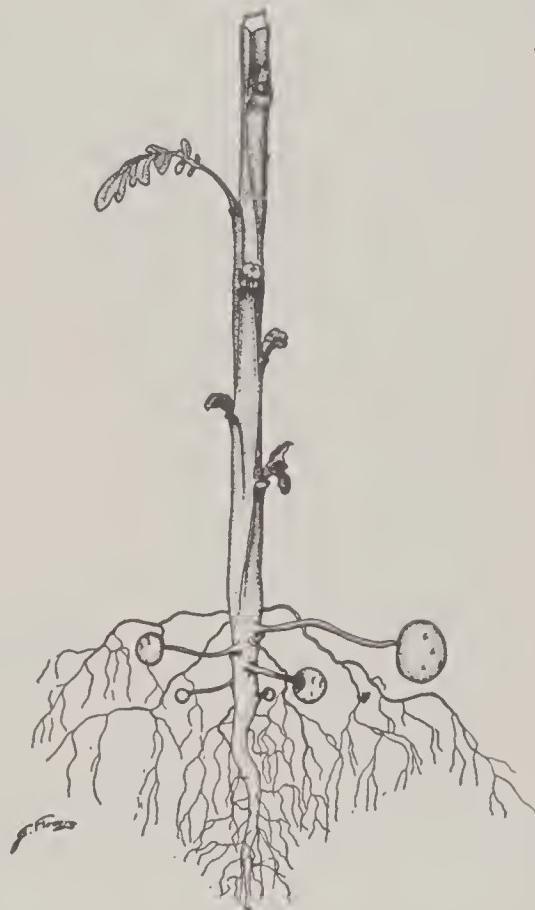


FIG. 271. Basal portion of potato plant showing development of rhizomes and young tubers.

than the central part of the lamina. Stomata are more numerous on the abaxial surface.

The leaves that develop on the subterranean portions of the stem are small and scale-like. Buds formed in the axils of these leaves produce rhizomes which elongate rapidly and develop tubers

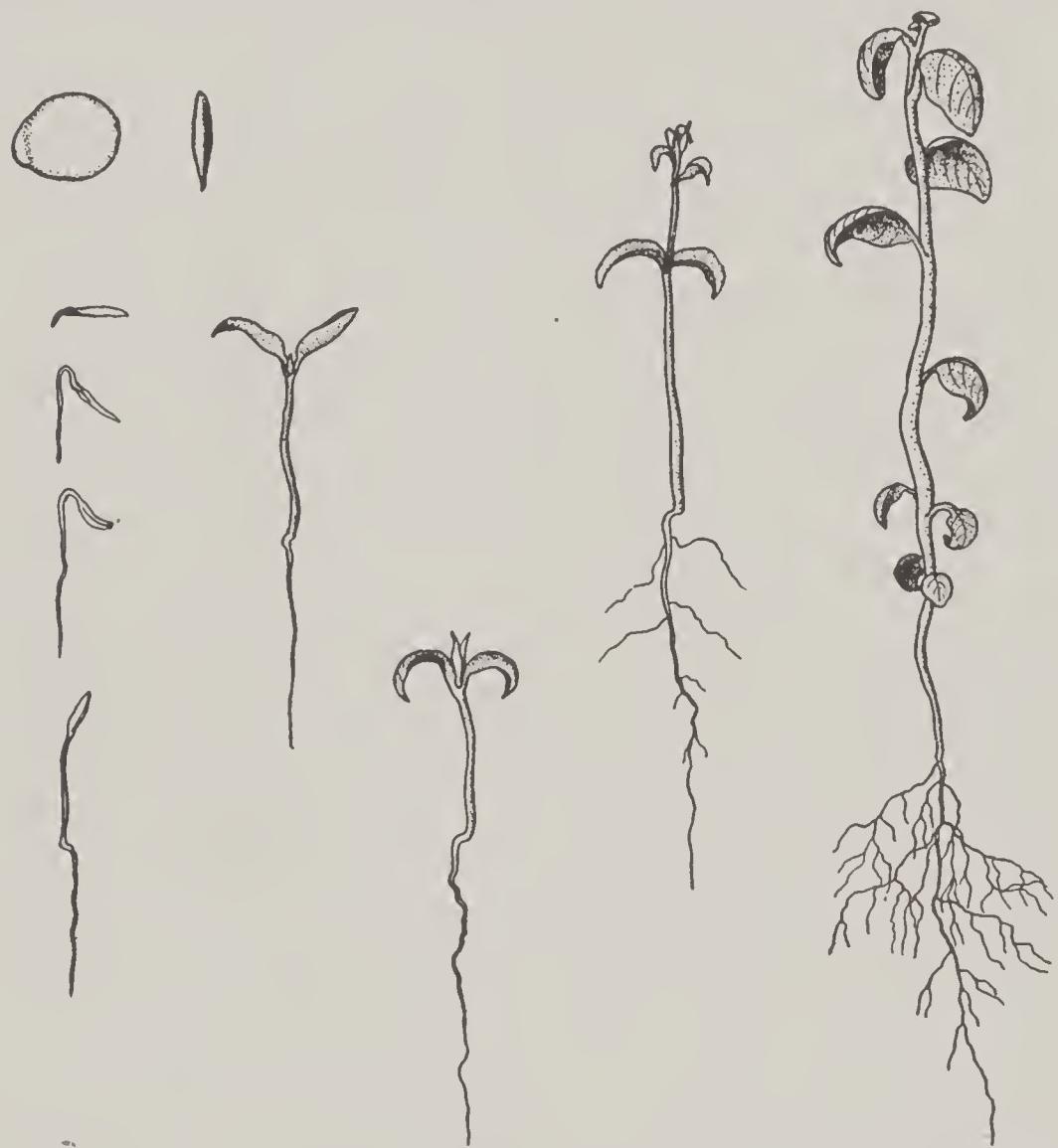


FIG. 272. Face and side view of potato seed and stages in development of seedling.

at their extremities. According to Clark (7), the rhizomes are variable in length, ranging from less than an inch to 18 inches, but they do not usually exceed 3 to 4 inches in cultivated varieties. The tuber is morphologically a fleshy stem bearing buds or "eyes" in the axils of small scale-like leaves which are soon shed, leaving a ridge or leaf scar subtending the bud.

Vegetative propagation results from the development of axillary buds which produce shoots, and these then give rise to adventitious

roots. Rosa (20) determined that the rapidity with which potatoes sprout is related to the maturity of the tubers at the time of harvesting, and noted that those harvested while immature emerge from dormancy more slowly than mature tubers. He also found that "The primordia of the vegetative sprouts develop during the later stages of tuber growth, as well as during the

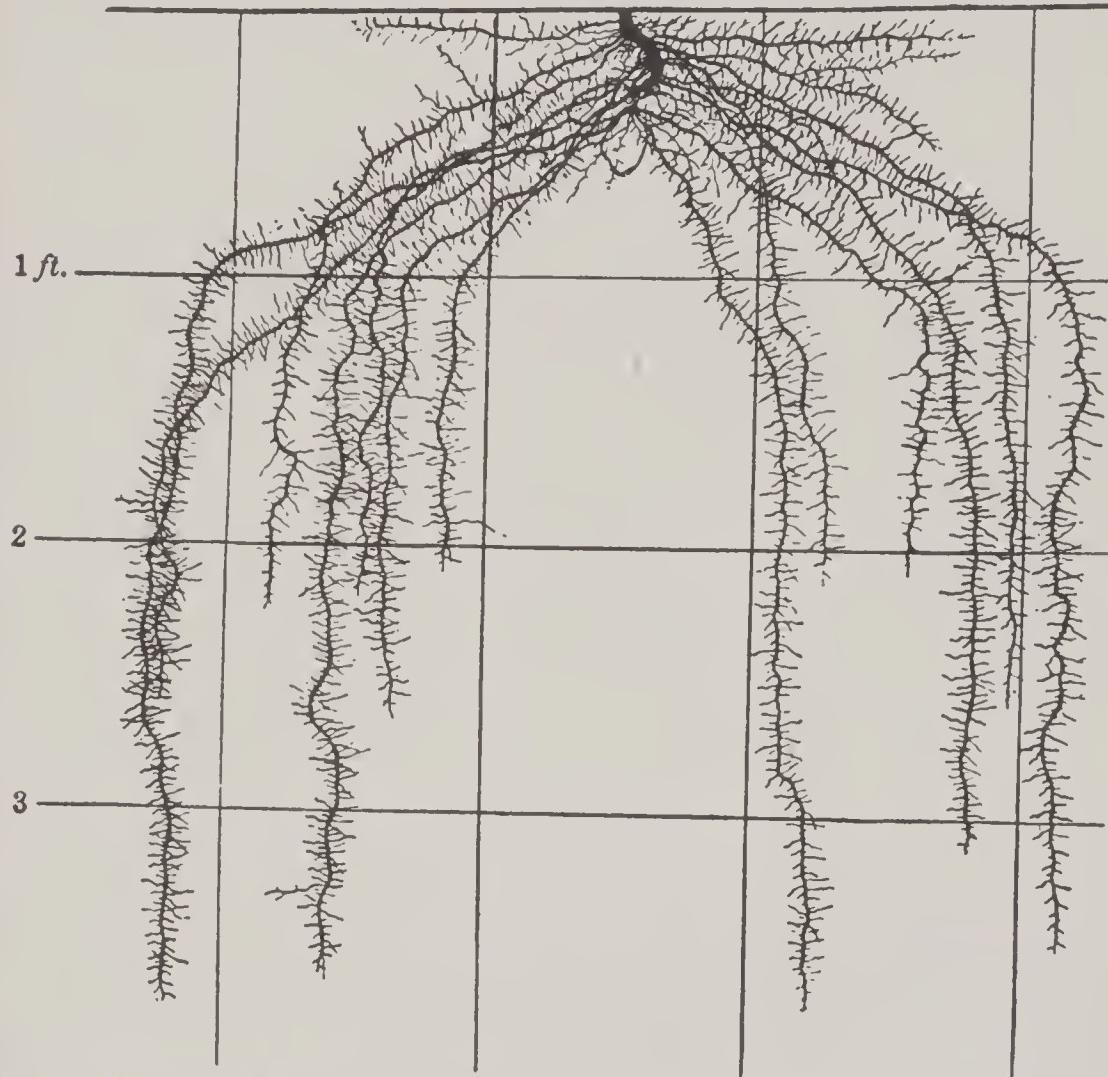


FIG. 273. The root of mature plant showing extent of one-half of total root system. (After Weaver, *Root Development of Field Crops*, McGraw-Hill Book Co.)

dormant period." The bud primordia are present even in very young tubers and there is a meristematic region, but the sprout does not begin to form until the later stages of tuber growth.

THE ROOT. — Plants grown from seed develop a slender tap root from which lateral branches arise to form a more or less fibrous system. (Fig. 273.) Those grown from tubers have a fibrous system consisting of adventitious roots that arise in groups of three at points just above the nodes of the underground stem. The root has been described by Weaver (28), who states,

"In its early growth, it is almost entirely confined to 8 inches of surface soil. After extending horizontally to a distance of 1 to 2 feet or more, the roots turn more or less abruptly downward and penetrate the second and third foot of soil. Roots may also occur in the fourth foot. Branching is very profuse throughout the root extent, and at maturity, laterals occur to the root tips. Usually the branches are relatively short but so numerous and well rebranched that the absorbing system is very efficient. There is some evidence which indicates that late-maturing varieties root deeper than early ones."

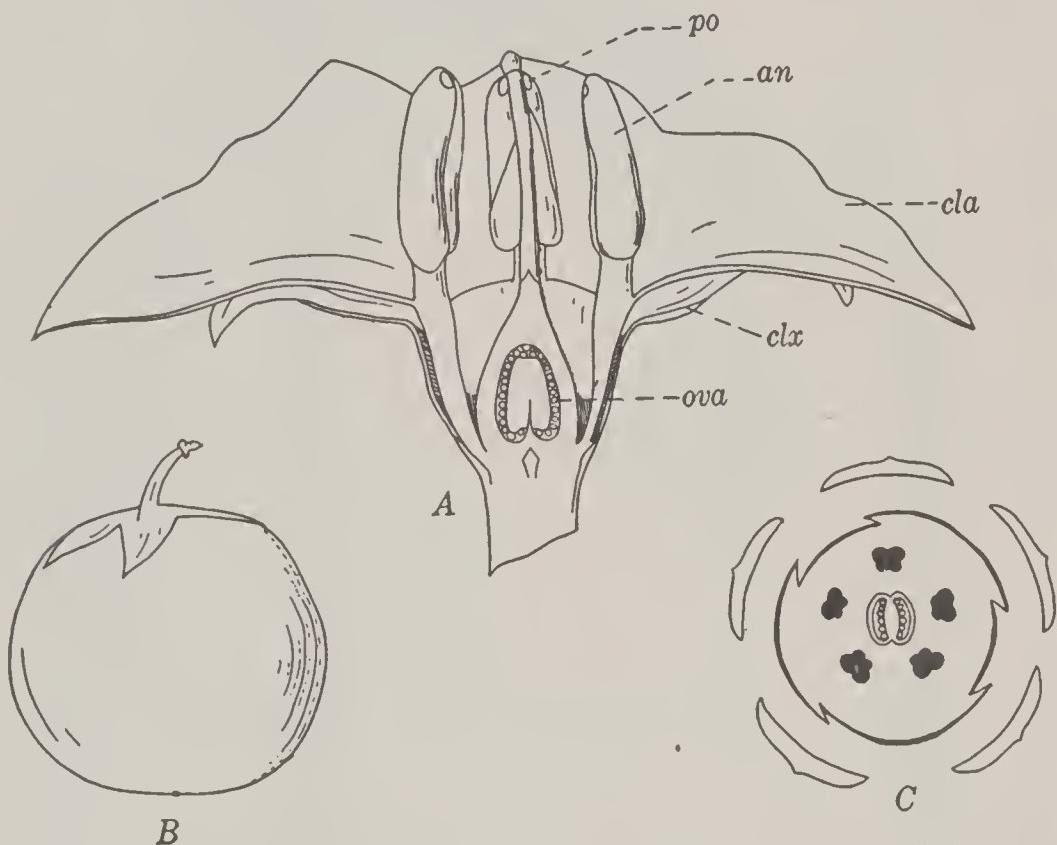


FIG. 274. A, median longisection of mature flower; B, berry; C, floral diagram: *an*, anther; *cla*, corolla; *clx*, calyx; *ova*, ovules; *po*, terminal pore of anther. (After Robbins, *Botany of Crop Plants*, P. Blakiston's Son and Co.)

THE INFLORESCENCE AND FLOWER. — The inflorescence is cymose and terminal although it appears to be lateral owing to the sympodial development of the axis. The five-merous flowers are white, yellow, purple, or blue and are borne on bractless pedicels. The calyx is tubular and lobed as is the gamopetalous corolla; and, at anthesis, the latter may be 1 to $1\frac{1}{2}$ inches in diameter. The stamens are alternate with lobes of the corolla and adnate to its tube. They are straight or slightly curved with large, erect, fleshy, yellow anthers that are longer than the filaments. Dehiscence of the anther is by means of two terminal pores. (Fig. 274, A, C.) The pistil consists of two undiverged carpels which

form a two-loculed ovary with a single style and stigma. The ovary is superior and the placentation axile.

The pollen is wind-borne, the flowers produce no nectar and are not visited by insects to any great extent, although Müller (15) has reported that bumblebees do visit them, obtaining some pollen. It seems probable that in most cases self-fertilization is natural and cross-pollination rare. Several types of sterility exist and East (11) has classified the varieties of potatoes into four groups with reference to this condition: (1) those whose flower buds fall without opening; (2) those in which a few flowers open but fall immediately; (3) those in which flowers persist for several days but lack viable pollen; and (4) varieties which flower freely, produce viable pollen, and bear fruits. Differences in environmental conditions may also induce varying degrees of sterility.

THE FRUIT. — The fruit is often referred to as a potato "apple," potato "ball," or "seed ball"; and is brown or purplish-green tinged with violet. (Fig. 274, B.) It is a two-celled, many-seeded berry, about $\frac{1}{2}$ inch in diameter, globular to oval in shape, and contains numerous small seeds that are attached to the thick axile placenta and are embedded in the green pulp of the fruit. Single fruits have been known to contain from 200 to 300 seeds; while in other cases no seed at all is produced.

ANATOMY

THE SEED. — The yellow to yellowish-brown seeds are small, flat, and oval or kidney-shaped. During development, the ovule arises from a massive placenta which is probably cauline, although in later stages the placentation appears to be foliar and axile. The orientation of the ovule is anatropous or partially campylotropous. Young (28) is of the opinion that the ovule does not have the typical anatropous form, since the nucellus and embryo are much curved, and has suggested that it represents a transition stage in the direction of campylotropy.

A single massive integument develops and there is a long micro-
pyle. Souèges (22) and Bhaduri (5) have investigated the histology of the integument and are in general agreement. At first the integument is only a few cells in thickness; but, as growth proceeds, it becomes massive and exhibits a definite differentiation of its tissues. Souèges has divided the fully mature integument into three layers: (1) an external region consisting of a single

layer of epidermal cells; (2) an intermediate zone which he divides into an external and internal region; and (3) an internal or digestive zone which forms the innermost layer of cells covering the endosperm. (Fig. 275, B, C.)

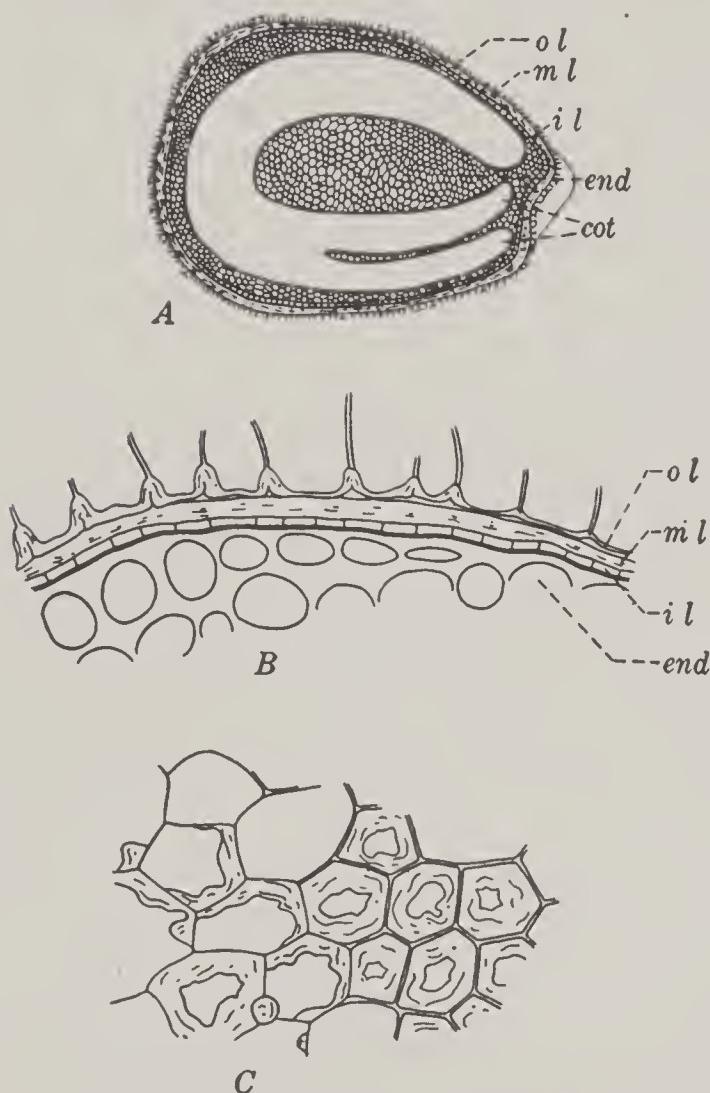


FIG. 275. A, median section through seed showing position of embryo; B, transection of portion of integument showing layers and part of endosperm; C, surface view of external layer of seed coat: *cot*, cotyledons; *end*, endosperm; *il*, inner digestive layer of seed coat; *ml*, middle partially digested and crushed layer; *ol*, outer layer showing hair-like projections of cell walls. (B and C, redrawn after Souèges, *Ann. Sci. Nat.*)

toward the surface. The cellulose bands are finally isolated through a gelatinization of the intervening wall substance with the result that hairs are formed on the surface of the mature seed. These are not true epidermal hairs, but the thickened portions of the epidermal cell walls which have been separated from one another.

As the seed develops and approaches maturity, definite changes occur in the character of the integument. The inner digestive layer acts as an haustorial zone, and there is a gradual digestion of the inner region of the middle layer which progresses centrifugally until nothing is left of the entire middle zone except a narrow band of much-crushed tissue. While the digestion of the intermediate zone of the integument is going on, a special type of wall thickening is taking place in the cells of the external layer. There is a deposition of cellulose on the inner tangential wall of each epidermal cell and the formation of longitudinal bands of cellulose which extend from the base of each cell

DEVELOPMENT OF THE SEEDLING. — The mature U-shaped embryo lies embedded in the endosperm so that both the tip of the radicle and those of the two cotyledons are directed toward the micropyle. (Fig. 275, A.) Upon germination, the radicle emerges from the micropylar end of the seed and grows rapidly to form a tap root which soon produces numerous secondary roots. The hypocotyl elongates, lifting the oval cotyledons above the ground;

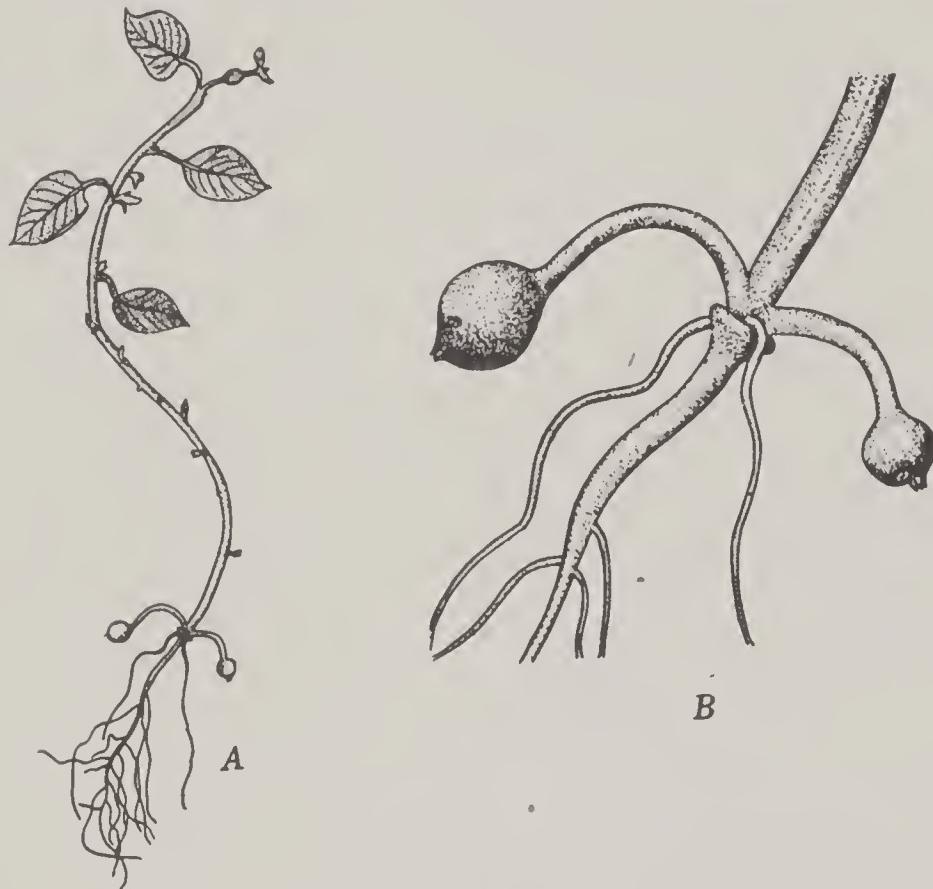


FIG. 276. A, habit of young seedling showing development of rhizomes and young tubers at cotyledonary node; B, enlarged detail of base showing rhizomes and adventitious roots at node.

and this is followed by the development of the epicotyl from which the first simple, ovate, foliage leaves are differentiated. (Fig. 272.)

At this time, the first rhizomes arise in the axils of the cotyledonary leaves above the ground level. They are slender and cylindrical, possessing small rudimentary leaves; and, after elongating until their tips strike the ground, they penetrate the soil and begin to swell and form tubers. (Fig. 276, A, B.) Adventitious roots arise from the rhizomes and the cotyledonary node, and additional rhizomes may develop in the axils of the first foliage leaves. In general, the tubers which are produced the first

year from seedlings are relatively small. There are reported cases in which large potatoes have been produced in one year from seed; but, ordinarily, normal tuber size for a given variety is not attained for about three years.

THE PRIMARY Root. — The young primary root has a diarch radial protostele. (Fig. 7.) The two protoxylem points abut the pericycle directly, and the metaxylem is differentiated centripetally to form a complete primary xylem strand early in the ontogeny of the primary axis. In some cases, a few fundamental parenchymatous cells may occur adjacent to the metaxylem; and, in others, there may be a small parenchymatous pith region. The first protoxylem elements to differentiate form annular or loosely spiral thickenings while the later ones have scalariform or scalariform-reticulate walls.

The primary phloem is radially arranged with respect to the protoxylem points, and the protophloem differentiates adjacent to the pericycle. Between the primary xylem strand and the two phloem groups is a zone of fundamental parenchyma in which the cambium is later differentiated. The stele is surrounded by an endodermis which exhibits well-developed Casparyan thickenings by the time primary maturation has been completed. The cortex consists of several rows of large parenchymatous cells with intercellular spaces, and the cortical cells are limited externally by an epidermis which bears root hairs.

ORIGIN OF LATERAL Roots. — Lateral roots arise early in the ontogeny of the primary root, and this is also true of laterals developed from the adventitious roots. They originate before or at about the time that the maturation of the primary xylem has been completed and just prior to the initiation of cambial activity. The first evidence of lateral root formation appears in the radial enlargement of the pericyclic cells which lie directly outside the protoxylem points or slightly to one side of them. This is followed by tangential divisions of the pericyclic cells, and further divisions in three planes result in the formation of the conical growing point of the lateral root. This growth forces the endodermis outward, and it finally ruptures, as do the cortical cells in the line of lateral root extension. The emergence of the root is accomplished in part by mechanical pressure and in part by the digestion of the cortical parenchyma. By the time the lateral root has elongated so as to reach the periphery of the cortex, a

definite root cap has been organized and the stelar elements have begun to differentiate against the primary xylem and phloem of the main axis. Direct contact with the primary vascular elements of the stele is possible owing to the point of origin of the lateral root and its early initiation.

ORIGIN OF ADVENTITIOUS Roots. — In commercial practice, the propagation of the potato, except for experimental work in potato-breeding, is accomplished by vegetative methods in which portions of the tubers, known as "seed pieces" or "seed", are planted. Vegetative growth results in the development of shoots, adventitious roots, and tubers. In this case, the entire root system is adventitious; and, as pointed out by Priestley and Swingle (17), the roots do not arise directly from the tuber, but originate from young sprouts which are formed by the development of the buds or "eyes" of the seed piece. These roots frequently occur in groups of three, and their point of origin is in the pericyclic region of the subterranean portion of the stele in close proximity to a nodal plate. As in the origin of laterals, the first evidence of adventitious root formation consists of an activation of the pericyclic cells, which first elongate radially and then divide tangentially. The endodermis keeps pace with the formation of the root primordium for a time, and later is broken when the endodermal cells cease division. Artschwager (1) states that the developing rootlet "pushes its way mechanically through the cortex, and is aided by the dissolving action of enzymes which are probably secreted by the cells of the endodermis."

The ontogeny of the lateral and adventitious roots is similar to that of the primary root except that they are not always diarch. Lateral roots are usually diarch, but adventitious roots may fre-

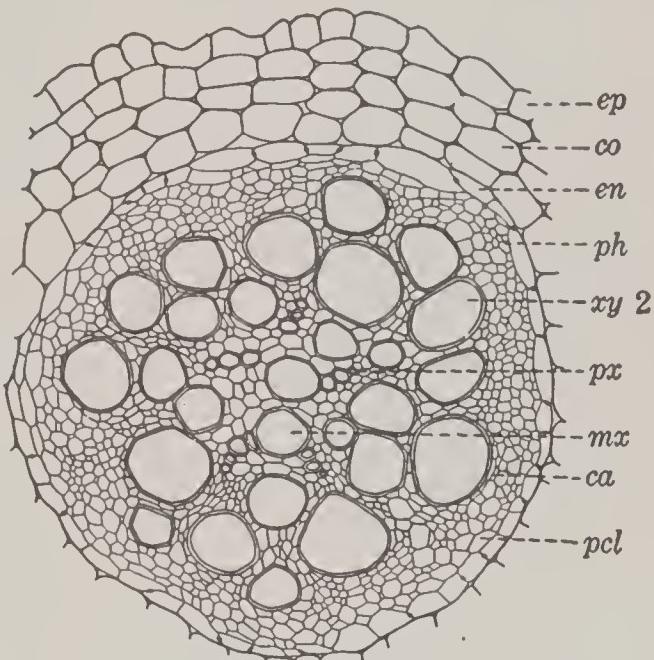


FIG. 277. Transection of adventitious root: *ca*, cambium; *co*, cortex; *en*, endodermis; *ep*, epidermis; *mx*, metaxylem; *pcl*, pericycle; *pb*, phloem; *px*, protoxylem; *xy 2*, secondary xylem.

quently be triarch or pentarch. (Fig. 277.) In all cases, the development of the primary xylem is centripetal and the arrangement of the primary phloem radial.

SECONDARY THICKENING OF THE ROOT. — At approximately the time that the primary xylem is mature, cambial activity is initiated in the parenchymatous zone between the xylem and the phloem, the first divisions occurring just outside the metaxylem portion of the strand. (Fig. 278.) From these loci there is a lateral extension of the cambial activity until it involves the pericyclic

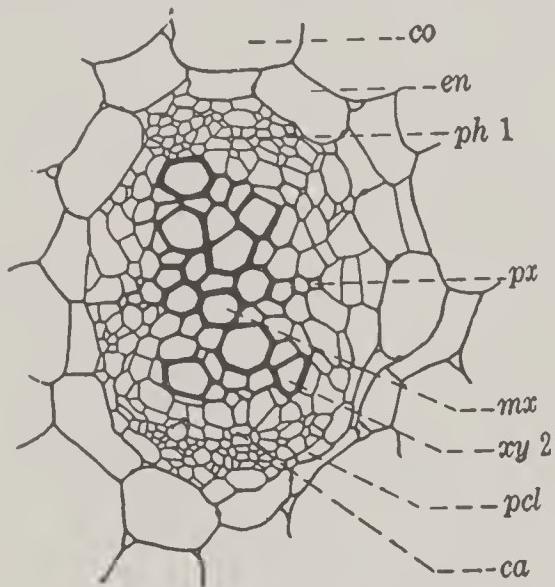
cells that subtend the protoxylem points. In this manner, a complete cambial cylinder is formed which produces secondary xylem elements centripetally and secondary phloem centrifugally. The cambium is relatively inactive and none of the roots of the primary or adventitious root systems attain large size.

The secondary xylem consists of vessels of two sizes, fibers, and parenchyma, while typical tracheids are absent. The large vessels are arranged in approximate radial rows, surrounded by parenchyma and vessels of smaller caliber. The tracheae are pitted, become filled with tyloses from cells. The few elongated fibers

FIG. 278. Young primary root after initiation of secondary thickening: *ca*, cambium; *co*, cortex; *en*, endodermis; *mx*, metaxylem; *pcl*, pericycle; *ph 1*, primary phloem; *px*, protoxylem; *xy 2*, secondary xylem.

and the larger ones frequently occur as scattered elements between the vessels.

As a result of secondary thickening, the primary phloem cannot be recognized in a transection of the mature root because of crushing and partial digestion. The secondary phloem consists of sieve tubes, companion cells, and parenchyma. No phloem fibers are differentiated. The relative inactivity of the cambium and the consequent slowness of secondary thickening result in a persistence of the cortex through a considerable period of the later ontogeny of the root. The parenchymatous cells of the cortex compensate for the increasing size of the stele by enlarging tangentially, but they do not divide to any great extent. In the



final stages of development, the epidermis and cortex become fissured and fragmented down to the endodermis. At such points, the endodermis develops thickenings on the inner tangential walls and the underlying pericyclic cells may divide tangentially to form a periderm.

VASCULAR TRANSITION. — The transition occurs in the hypocotyl and cotyledonary petiole. It involves a reorientation of the stelar elements, which is here described beginning at the root-like por-

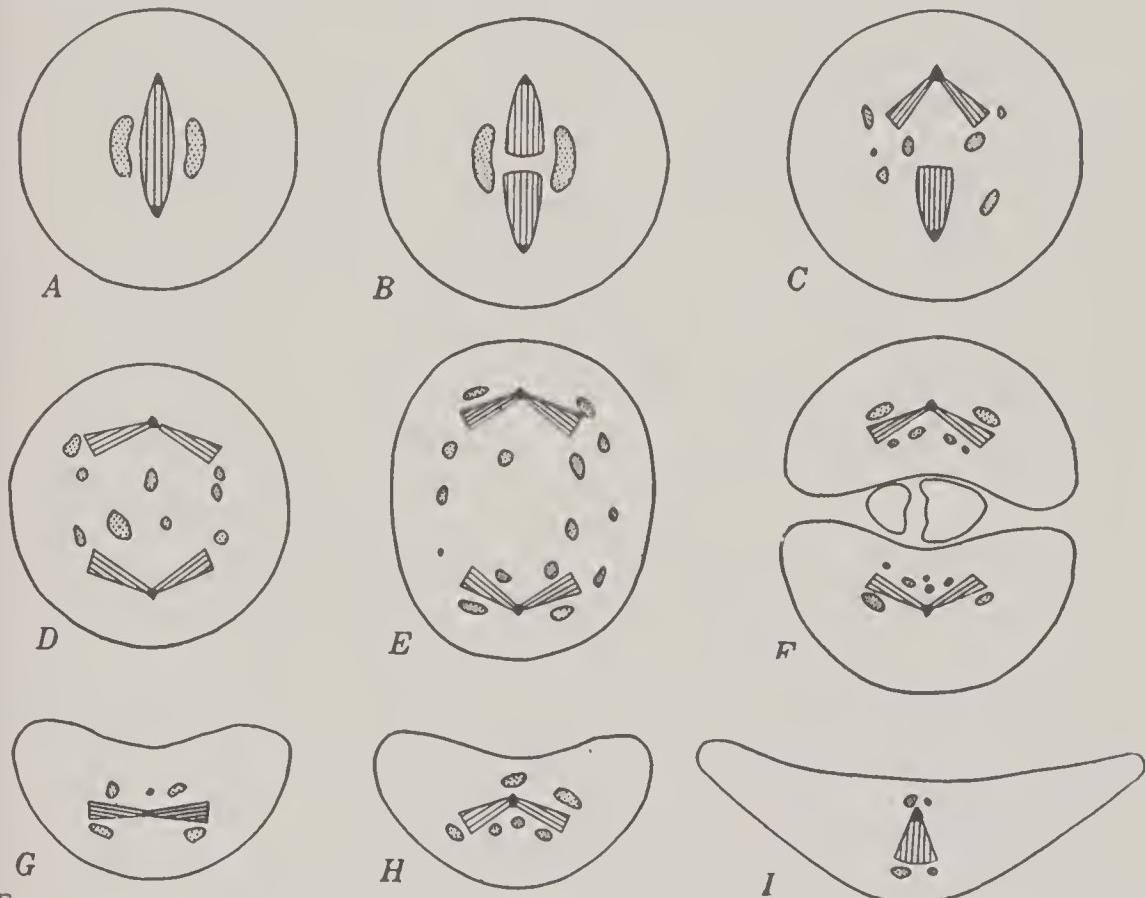


FIG. 279. A-I, diagrams representing vascular transition. Dotted areas indicate primary phloem; solid areas, protoxylem; lined areas, metaxylem. (Adapted after Theil.)

tion of the lower hypocotyl and proceeding in an ascending direction to the cotyledons.

The first variation from the diarch radial protostele is the division of the protoxylem strand into two sectors owing to the fact that the cells of the central region remain parenchymatous instead of differentiating into metaxylem. (Fig. 279, B.) At the same level, each of the primary phloem regions subdivides into two or three distinct groups. Above this point, there is a change in the direction of differentiation of the later formed proto- and metaxylem; which, instead of being laid down centripetally, on the same radius as the protoxylem, is differentiated to the right

and left of the protoxylem points in a more or less tangential direction so that each metaxylem group is bifurcated. (Fig. 279, C, D.)

Artschwager (1) describes and figures this stage in the transition as a swinging of the two protoxylem groups in an outward direction, "one group following a left, the other a right curve"; but Thiel (24) agrees with the description given above. In the upper hypocotyl, the bifurcation of the metaxylem becomes more pronounced until, at the level of the node, each cotyledonary trace consists of a group of protoxylem cells with metaxylem elements lying on either flank at an approximate right angle to the plane of the protoxylem poles. (Fig. 279, E.)

While this reorientation of the primary xylem is taking place, definite changes occur in the position of the primary phloem. The central group of cells from each original phloem group diverges gradually toward the center of the stele; and, ultimately, constitutes the inner phloem of the bicollateral bundles of the cotyledons. (Fig. 279, C, D, E.) The remaining groups of phloem incline tangentially in the direction of the protoxylem points until they occupy a position at the periphery of the stele and adjacent to them. The number of phloem groups increases, and some of the strands come to lie in a position outside the proto- and metaxylem. The inner phloem groups also increase in number; and, as the medullary region enlarges, they occupy a position on the inner face of each double bundle. In this manner, the bicollateral bundle of the cotyledonary trace is established. (Fig. 279, G.)

The position and direction of development of the proto- and metaxylem at the cotyledonary node is not strictly endarch, although the protoxylem may be nearer the periphery than the metaxylem. (Fig. 279, H.) At the base of the cotyledonary petiole, the midvein consists of protoxylem and two groups of laterally placed metaxylem with adaxial (inner) phloem on one face of the xylem and several strands of abaxial (outer) phloem on the other. In the lamina of the cotyledon, the protoxylem is differentiated in a more nearly adaxial position with reference to the metaxylem until ultimately the endarch orientation is attained. (Fig. 279, I.) The amount of adaxial phloem gradually decreases toward the distal portion of the midvein; and, in the smaller bundles, it may disappear completely so that they are collateral instead of bicollateral.

ONTOGENY OF THE STEM. — Artschwager (1, 2) has investigated the ontogeny and vascular anatomy of the stem and tuber, and the following account is based upon his report. The first differentiation in the apical meristem is the demarcation of the dermatogen, a peripheral layer of cells giving rise to the epidermis; and the appearance of the procambial ring that separates the parenchymatous tissue of the pith from that of the cortex. The procambial ring is the forerunner of the stele; and the small, elongated, thin-walled cells which comprise it are filled with a dense cytoplasm. They are readily distinguished from the adjacent parenchymatous cells of the cortex and pith which are less dense, much larger, and more nearly isodiametric.

As the leaf primordia arising from the growing point of the stem undergo growth and development, the downwardly differentiating bundles of their traces first appear in the procambial ring. The first vascular elements to mature are the protoxylem cells located in the median zone of the procambial cylinder. They are long and slender and have annular wall thickenings in which the rings are spaced at a considerable distance from one another. Some of the protophloem cells may differentiate simultaneously with the development of the protoxylem, but they are not structurally different from the adjacent procambial cells and cannot be distinguished from them. Shortly after the formation and development of the protoxylem, the inner phloem is differentiated.

There is a centrifugal development of the succeeding primary xylem elements so that they are endarch in orientation. The later-formed protoxylem elements are somewhat larger than the initial ones, and their secondary wall thickenings are characterized by a series of close rings or loose spirals. As differentiation proceeds, groups of phloem initials are formed in the outer portion of the procambial zone. These are similar to, but less numerous than, those differentiated earlier in the procambial region adjacent to the pith. The cells of the undifferentiated portion of the procambial ring, between the primary xylem and the outer phloem, appear very regular in arrangement owing to a series of tangential divisions which mark the initiation of cambial activity. This activity does not at first result in the formation of a continuous ring, and at this stage there is a series of discontinuous sectors of fascicular cambium lying on the same radii as the primary xylem and phloem groups.

The slightly elongated cells of the inner phloem are rich in cell contents, and the behavior of the cytoplasm in fixed tissue suggests that there are cytoplasmic connections between adjacent protophloem elements in the same vertical series, although actual perforations cannot be detected. Following the development of

the inner protophloem, further differentiation is centrifugal and sieve tubes occur in the later-formed metaphloem groups. Somewhat later, sieve tubes also develop in the outer phloem groups. These are similar to those of the inner phloem, but they are laid down centripetally instead of centrifugally.

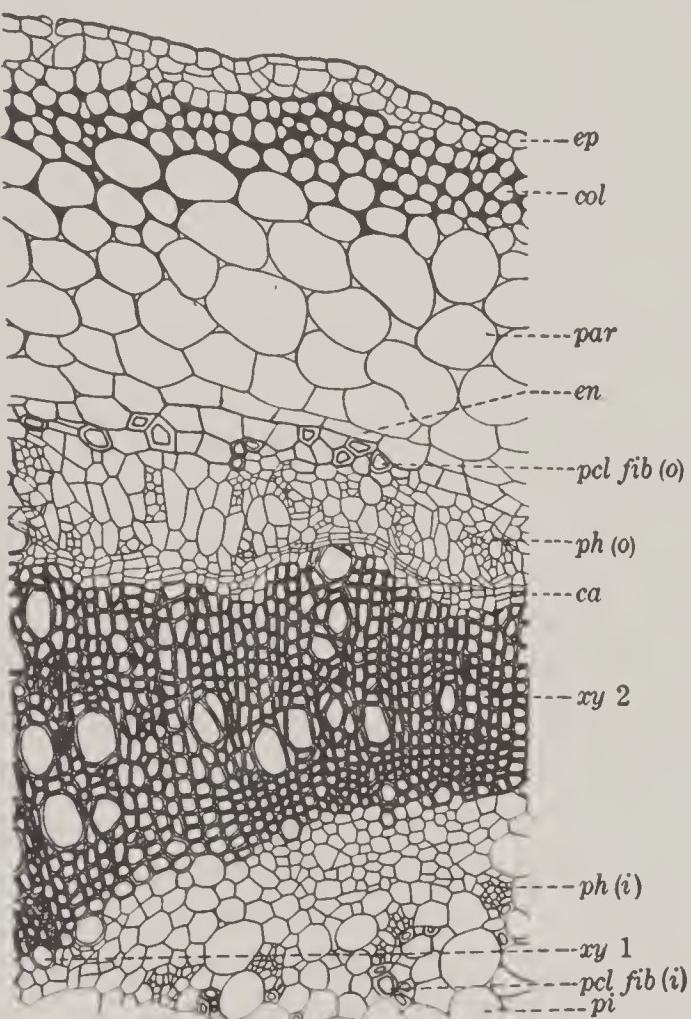
Coincident with the progressive development of the phloem groups, the protoxylem becomes more extensive and the elements formed have closely spaced rings and flat spirals. Continued development results in the formation of larger metaxylem elements with scalariform or scalariform-reticulate walls.

As the primary xylem is

FIG. 280. Transection of sector of mature stem: *ca*, cambium; *col*, collenchyma; *en*, endodermis; *ep*, epidermis; *par*, parenchyma; *pcl fib (i)*, inner pericyclic fibers; *pcl fib (o)*, outer pericyclic fibers; *ph (i)*, inner phloem; *ph (o)*, outer phloem; *pi*, pith; *xy 1*, primary xylem; *xy 2*, secondary xylem.

differentiating, the inner phloem groups increase in size and the outer ones become larger and more distinct.

While the maturation of the primary tissues of the vascular bundles is still taking place, there is an activation of the fascicular cambium which forms a distinct region prior to the differentiation of well-defined sieve tubes in the inner phloem. Subsequent divisions of the cambial initials result in the formation of two or three layers of cells between the primary xylem and the



outer phloem. In the differentiation of the primary vascular system, six major bundles are formed which are separated by medullary rays consisting of fundamental parenchyma; and, later, an interfascicular cambium develops across them, although this does not take place simultaneously at all points. While the interfascicular cambium is being formed, there is also a lateral extension of groups of outer and inner phloem. The outer groups are small and rather closely arranged while the inner groups are more widely separated from one another. (Fig. 280.)

At this time, changes also occur in the epidermis and cortex. The epidermal cells become cutinized and guard cells are formed. Within the epidermis are one or two layers of vertically elongated parenchymatous cells, and centrad to these is a zone of collenchymatous elements with thickenings at their angles and on the radial and tangential walls. Centrad to the collenchyma, the cells are large and there are numerous intercellular spaces. The cortex is limited centripetally by an endodermis, and Casparyan strips develop at about the time that the collenchyma matures.

Among the last tissues to differentiate are the pericyclic fibers which arise immediately adjacent to the endodermis, and fibers also develop in the perimedullary zone inside the inner phloem groups. These have been regarded by some investigators as phloem fibers; but others, who interpret the stele as an amphiphloic one with an inner pericycle, have considered them to be pericyclic in origin. The perimedullary zone is a band of parenchymatous tissue lying between the inner phloem and the primary xylem which consists of small compact cells that are derived from the procambial ring.

THE MATURE STEM. — The mature stem is subtriangular or quadrangular in transection. This results from the development of three large vascular bundles and the wing-like projections of the leaf which extend down the stem from each node because of the decurrent habit of the petiole. Between each pair of major bundles are three smaller ones; and, in the mature stem, a continuous cylinder of vascular tissue is formed by the development of an interfascicular cambium. The stelar region is limited outwardly by the endodermis and inwardly by scattered groups of pericyclic fibers, which become more or less irregularly oriented on its inner margin owing to the inequalities of cell division and enlargement in this region. (Fig. 280.)

The histology of the proto- and metaxylem has been described. The secondary xylem is laid down in radial rows, and consists of large vessels, tracheids and parenchyma. The former are heavily pitted with the pits arranged in transverse series, and each vessel segment is two or three times longer than broad. Parenchymatous cells surround the vessels, and are also laid down in radial rows as xylem rays.

The mature sieve tubes are cylindrical, and a single sieve plate comprises the entire transverse wall. Each plate is perforated by a large number of circular pores, but these do not have sieve fields such as occur in some phloem types. No plates occur on the radial and tangential walls. The inner and outer phloem elements are approximately equal in size, and the sieve tube segments do not vary much in length except that the segments are short and relatively broad where anastomoses of bundles occur.

In general, the sieve tube arises from an initial which undergoes longitudinal division to form two cells of unequal size, a large sieve tube and a smaller companion cell, but there may be variation in this respect. In some cases, the sieve tube initial does not undergo longitudinal division so that there may be a series of sieve tubes without adjacent companion cells. In addition to the sieve tubes and companion cells, phloem parenchyma is differentiated. These cells are elongated and rectangular, with simple pits in their end walls unlike the sieve plates of the sieve tubes.

The pericyclic fibers have pointed ends and are long and awl-shaped with a small lumen and heavily thickened unpitted walls that later become lignified. The endodermal cells are longer in the tangential dimension than in the radial one and Caspary strips are present but not well differentiated.

VASCULAR ANATOMY OF THE STEM. — Each leaf trace consists of five bundles and at the base of the semicircular petiole there are three large centrally located bundles and two smaller ones which lie at its outer edges. The course of the bundles in the stem is illustrated in the accompanying figure. (Fig. 281.) In this figure, *A*, *B*, and *C* indicate the main bundles, while *a* and *b* represent two of the three smaller bundles. The smaller intermediate bundles, *a* and *b*, become median traces of the leaves. Branches of the three large bundles *A*, *B*, and *C* form the four lateral bundles of the leaf traces. The traces to the wings of the

petiole are derived from further branching of the lateral groups, B^2 and A^4 , after these have become separated from the stem bundles. Artschwager's summary of the course of the bundles follows:

"(1) The median trace ascends without fusion or forking through three internodes, and then passes into the petiole without branching.

"(2) The lateral traces are given off at the node from two of the three large stem groups.

"(3) Each large stem bundle ascends without branching in turn for two internodes or for one internode.

"(4) Where a large stem bundle ascends for but one internode without branching, it divides three times, giving rise upon the first division to a new stem bundle, upon the second division to a new median trace, and upon the third division to lateral traces of the petiole. Upon the division in the node, half of the tissue is given off to unite with that from the left (in a right spiral) adjacent group, forming a new large bundle directly above the insertion of the leaf. Where the bundle ascends for two internodes without branching, it gives off vascular tissue only for lateral traces of the petiole.

"(5) Each leaf derives its supply from two large bundles and the smaller one lying between these. The method of derivation is uniform for all leaves, the bundles taking part being each time a different pair from those supplying the leaf below. In a right spiral the right member of the set supplying a leaf supplies also the leaf above, becoming there the left member of the set. The median trace of a given leaf is formed just below the third node below the leaf it supplies."

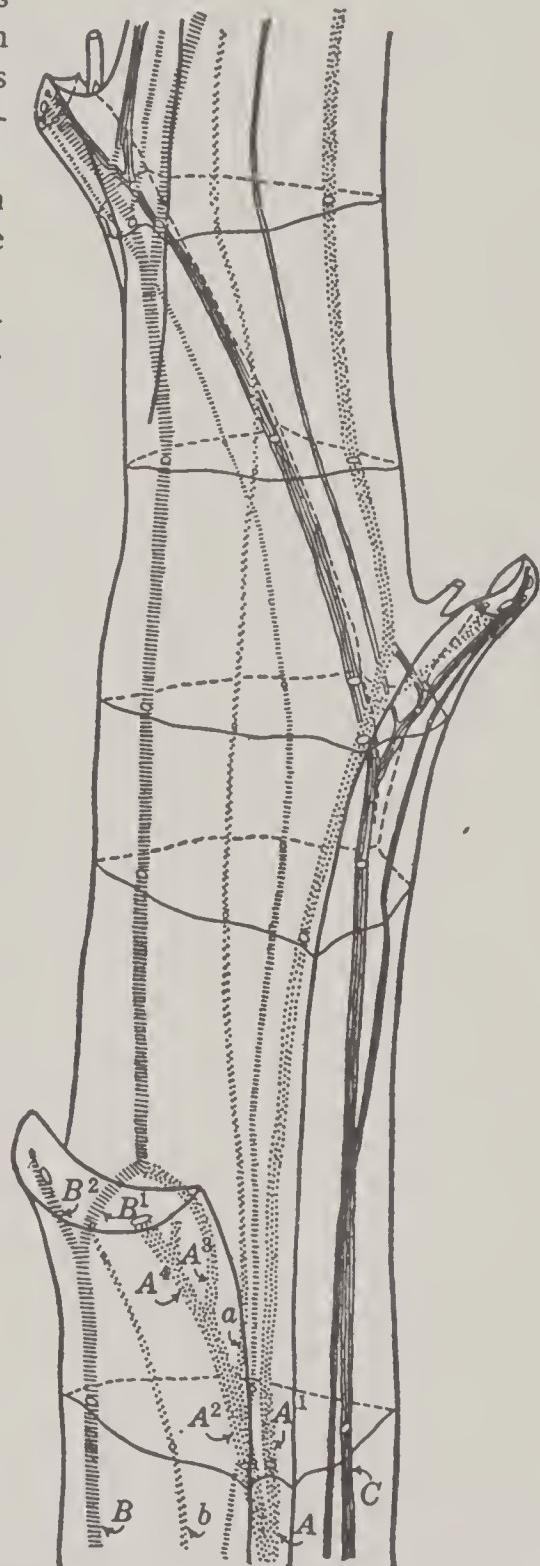


FIG. 281. Diagrammatic longisection of stem showing course of vascular bundles and vascular supply to leaves. (After Artschwager, *Jour. Agr. Res.*)

The subterranean portion of the stem is similar to the aerial in general plan, but differs from it in certain characteristics. There is a decrease or complete absence of collenchyma in the cortex; and immediately beneath the epidermal layer, the cells tend to become more or less thickened at points where the epidermis is ruptured. The epidermal cells are heavily suberized and Casparyan strips in the endodermis are clearly defined.

ANATOMY OF THE RHIZOME. — The rhizome is stem-like, and its ontogeny resembles that of the aerial shoot. The meristem has the three zones, dermatogen, procambium, and fundamental meristem, that occur in the aerial stem. The dermatogen forms a single-layered epidermis consisting of square or hexagonal cells that are at first approximately isodiametric, but later become elongated in the axial direction. The outer wall is somewhat arched and is thicker than the inner one with a thin cuticle. Some of the epidermal cells are specialized to form guard cells and hairs, and both stomata and hairs are produced in limited numbers but are ephemeral because of the early development of the periderm.

The cells of the meristem enlarge without differentiation to form the cortical zone external to the procambial ring and the medullary zone within it. The cortex consists of a band of parenchymatous cells eight or nine layers in width which are rounded and isodiametric or slightly elongated. Near the periphery, the cells tend to be collenchymatous, but to a much less degree than in the aerial stem. Small intercellular spaces are formed between the cells in the middle cortical region. The cells adjacent to the endodermis are smaller and approximately the size of the endodermal cells in tangential dimension. The first visible storage product, starch, can be detected in the cells adjacent to the procambial ring; and, later, larger deposits occur in the intermediate cortical cells. The peripheral cells are usually devoid of starch, but protein granules occur in increasing abundance as the maturation of the tuber proceeds.

The pith of the young rhizome is small as compared with the cortex, and the cells comprising it are axially elongated. Both pith and cortical cells are profusely pitted with groups of simple pits. The development of the vascular tissue from the procambium is similar to that of the aerial stem, but there is proportionately more phloem produced than xylem. The outer phloem groups

form a nearly continuous band limited externally by pericyclic parenchyma which in turn is bounded by the endodermis. The inner phloem groups are separated from the xylem by thin-walled cells of the perimedullary zone. Between the outer phloem and the primary xylem, there is a single layer of procambial tissue which later functions as a cambium and gives rise to secondary xylem and phloem.

In the young rhizome, the primary xylem consists of a few scattered annular and spiral elements surrounded by parenchyma. (Fig. 282.) These initial elements occur very close to the apex of the rhizome, and the elongation of this portion of the axis results in a stretching of the protoxylem elements until the lumen of the vessel may be closed owing to the flattening of the lateral walls. The later formed primary xylem consists of vessels with close spiral thickenings or shorter, scalariform elements. The phloem cells are similar in form and development to those described for the aerial stem. The cambium first appears in the vascular regions of the procambial cylinder; but, later, it forms a nearly continuous zone which produces a limited amount of secondary vascular tissue.

In that part of the rhizome which forms the connecting link between the stem and the tuber, the endodermis is very well defined with prominent Caspary strips, and there also may be a suberin layer deposited over the inner tangential walls of its cells. Unlike the portion which tuberizes, the epidermis persists, and its outer walls as well as the epidermal hairs may become lignified. The accompanying diagram (Fig. 283) indicates the proportionate amount of tissue found in each zone of the mature rhizome, and Artschwager (2) has computed the relative areas of each type of tissue.

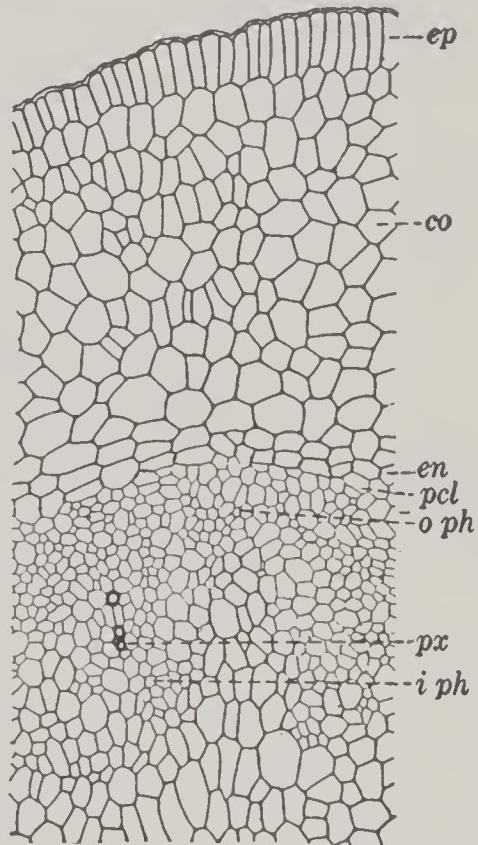


FIG. 282. Transection of tip of young rhizome showing a few annular and spiral elements of protoxylem surrounded by parenchyma: *co*, cortex; *en*, endodermis; *ep*, epidermis; *i ph*, inner phloem; *o ph*, outer phloem; *pcl*, pericycle; *px*, protoxylem. (After Artschwager, *Jour. Agr. Res.*)

TABLE IV

RELATIVE AREAS OCCUPIED BY THE DIFFERENT TISSUES OF THE CROSS SECTION OF A MATURE RHIZOME

RHIZOME TISSUES MEASURED	AREA (SQ. MM.)	PER CENT OF TOTAL
Cross-sectional area of rhizome	2.130	100.0
Cross-sectional area of outer phloem277	
Cross-sectional area of inner phloem239	{ 24.2
Cross-sectional area of xylem174	8.2
Cross-sectional area of pith350	16.3
Cross-sectional area of cortex	1.090	51.2

(After Artschwager)

It will be noted from this table that the total transectional area of the outer phloem exceeds that of the inner, and that the two combined are approximately three times the area of the xylem,

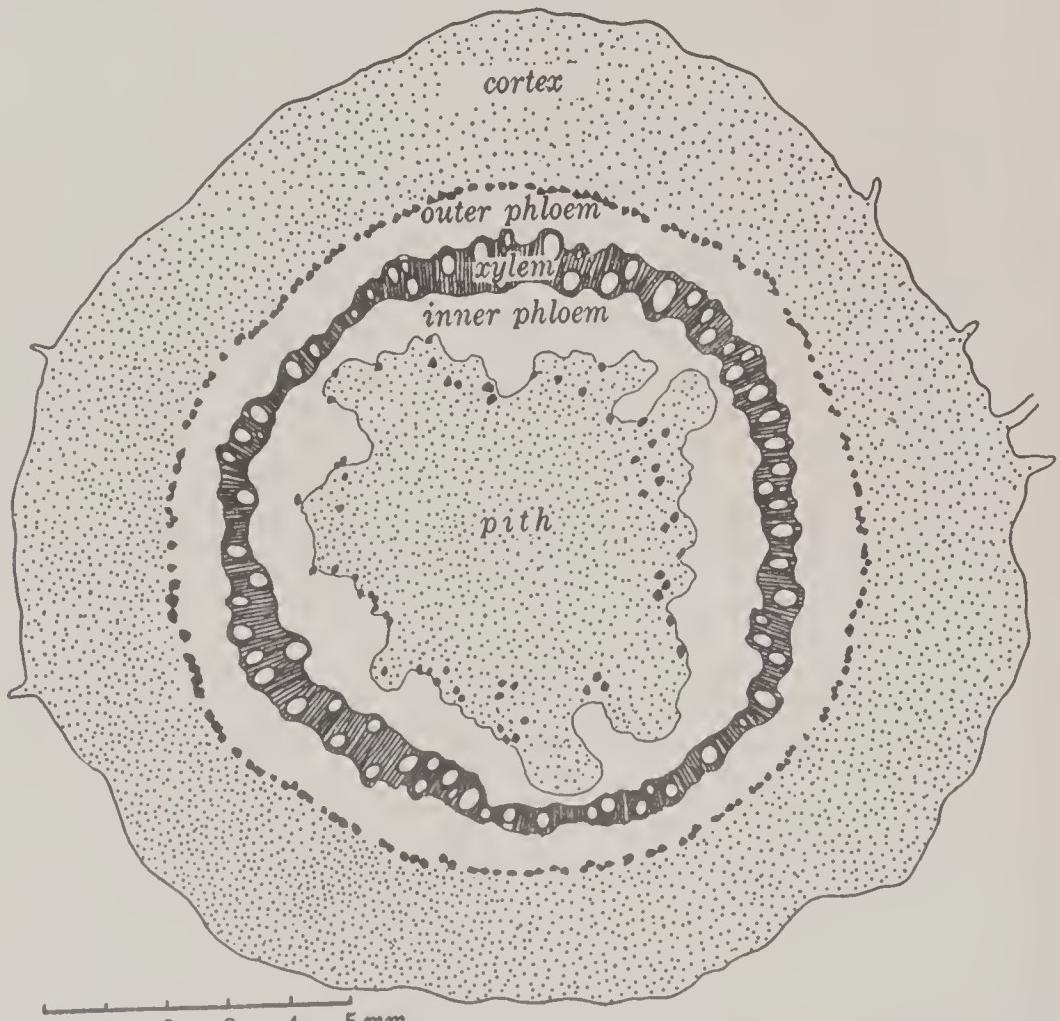


FIG. 283. Diagrammatic transection of mature rhizome showing proportional amount of tissue in the principal zones. (After Artschwager, *Jour. Agr. Res.*)

while the parenchymatous tissues of pith and cortex comprise nearly two-thirds of the total area.

Crafts (9) has investigated the structure of the phloem in relation to the problem of translocation. He rejects theories to account for the rapid transport of carbohydrates to the tuber that are based upon diffusion, protoplasmic streaming, or movement through young sieve tubes, conducting parenchyma, and perforations in



FIG. 284. Basal portion of plant showing habit of mature tubers. (Photograph by J. Horace McFarland Co.)

sieve plates. Instead, he proposes that "Diffusion along plasmodesma of cross walls and acceleration by protoplasmic streaming within non-vascular tissues, combined with pressure flow through permeable sieve tubes and phloem walls within specialized conducting organs, seem most satisfactorily to explain translocation in the potato."

ANATOMY OF THE MATURE TUBER. — The mature tuber is morphologically a short thickened stem bearing scale leaves that fall off early in ontogeny, leaving prominent scars. (Fig. 284.) In

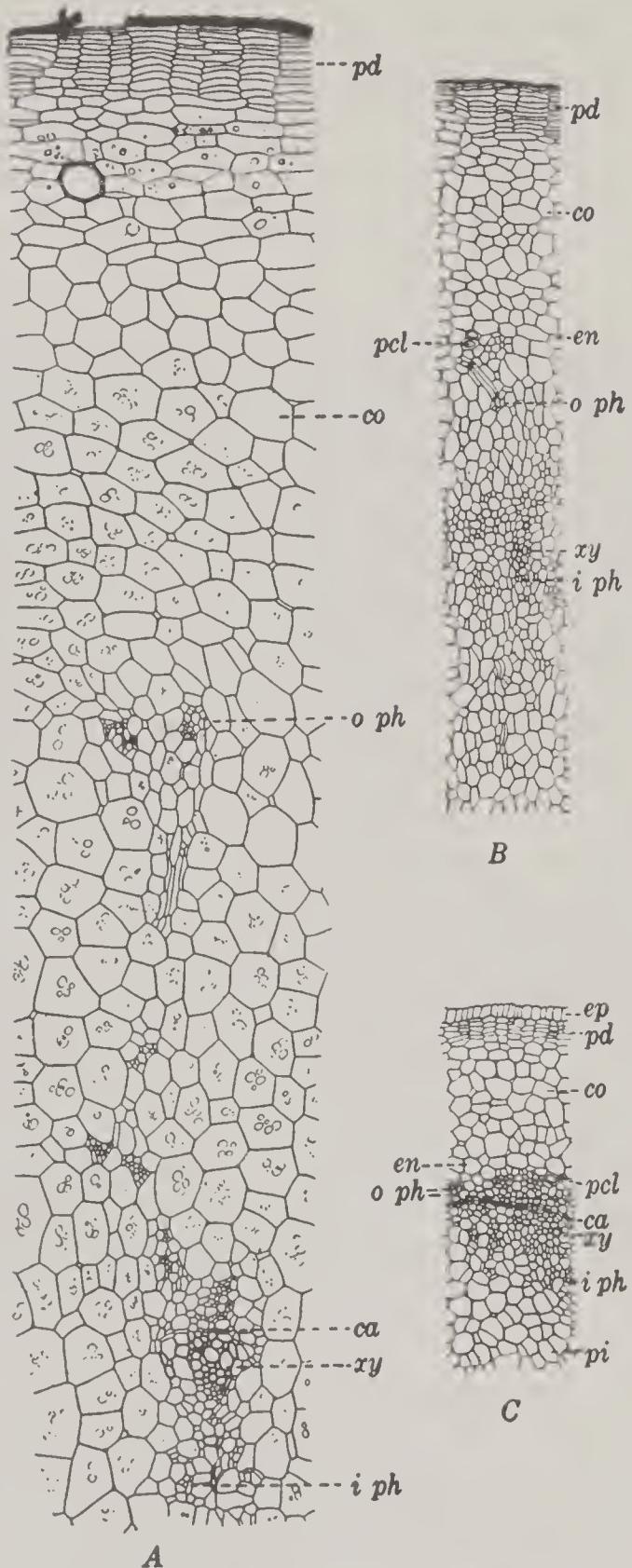


FIG. 285. Stages in development of tuber: A, transection through periderm, cortex, pericyclic region, and vascular ring of mature tuber; B, same region as in A, tuber 10 mm. in diameter; C, same as in A and B, tuber 2.5 mm. in diameter: ca, cambium; co, cortex; en, endodermis; ep, epidermis; i ph, inner phloem; o ph, outer phloem; pcl, pericycle; pd, periderm; pi, pith; xy, xylem. (After Artschwager, *Jour. Agr. Res.*)

the axil of each leaf is a compound bud consisting of an unelongated branch bearing several rudimentary leaves and axillary buds. The central bud, which is the most prominent, is the first to develop when growth is resumed. The arrangement of the leaves is spiral and agrees with the phyllotaxy of the vegetative stem.

Tuberization results from a cessation of the polar growth of the axis of the rhizome and a marked lateral proliferation of storage tissues which form the main bulk of the mature tuber. The anatomy of the tuber has been variously interpreted. De Vries (26), in his classic work on the potato, regarded the tissue of the tuber as being chiefly vascular and derived from the cambium, differing from the normal cambial product only in that the parenchyma produced was thin-walled storage tissue rather than woody parenchyma. Esmarch-Bromberg (12) attributed the principal growth of the tuber to an enlargement of the medullary region, and regarded the inner phloem groups as having an independent origin unrelated to the vascular cylinder. Reed (18) ascribed the growth of the tuber to the activity of three parenchymatous regions, the medulla, phloem, and cortex; and Artschwager (2) is in essential agreement with Reed except with reference to the activity of the inner phloem parenchyma. In regard to this region, Reed states that the cells between the inner phloem and the protoxylem begin to divide very early in ontogeny, causing a spreading out or dispersion of the phloem groups. He also holds that the parenchyma of the inner phloem groups is very active, contributing a considerable amount of tissue to the growing tuber. Artschwager expresses doubt on this point, and attributes the increased amount of storage parenchyma to the proliferation of cells in the procambial zone, especially in the perimedullary region, rather than to an activity of the parenchyma of the inner phloem.

The principal zones in the mature tuber from the periphery inward are the periderm, cortex, vascular cylinder, perimedullary zone, and central pith. (Fig. 285, A.) The periderm is six to ten cell layers in thickness and acts as a protective zone over the entire tuber, being broken only by small lenticel-like structures. These develop in the tissue underlying the stomata and are initiated when the young tuber still retains its epidermis. There is considerable variation in the width and character of the periderm in different varieties of potatoes, some of which are sufficiently

constant to be of diagnostic value in describing types. In most cases, however, individual variations under a wide range of cultural conditions indicate that the character of the periderm is too plastic to be of use in this connection.

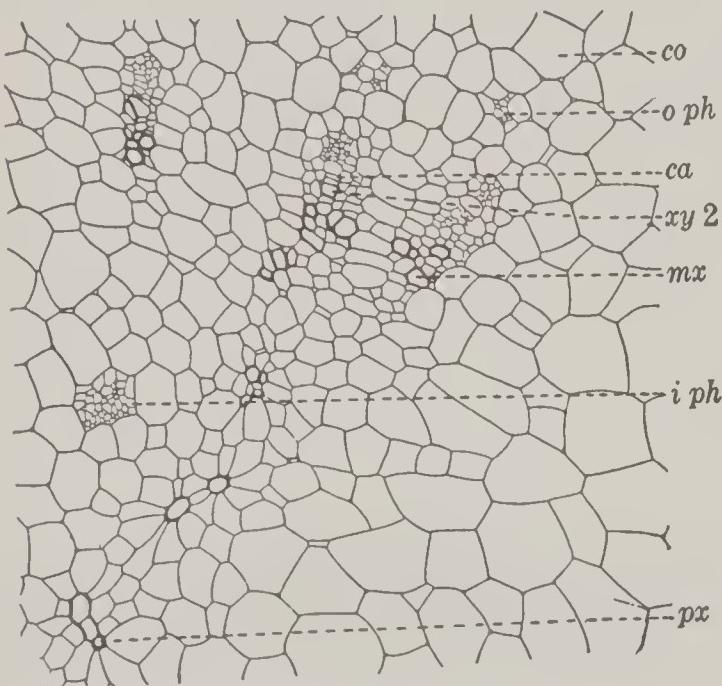
The cortex consists of a narrow band of storage tissue within the periderm, and its peripheral cells contain tannins, protein crystals, and a limited amount of starch in addition to pigment in the colored varieties. The pith forms a small central core from which radiate arms of medullary parenchyma so that this region appears irregularly stellate in transection. The cells are relatively

low in starch content, have a greater proportion of water, and appear more translucent than adjacent tissues.

The vascular cylinder lying between the cortex and the perimedullary zone is narrow, containing secondary xylem and phloem outside of which the outer primary phloem forms a relatively limited storage region. Centrad to the vascular ring is the major region of storage parenchyma. This is derived from the inner portion of the procambium and constitutes the perimedullary region in which numerous groups of inner phloem are located. (Fig. 286.)

FIG. 286. Transection through portion of vascular tissue of mature tuber: *ca*, cambium; *co*, cortex; *i ph*, inner phloem; *mx*, metaxylem; *o ph*, outer phloem; *px*, protoxylem; *xy 2*, secondary xylem. (After Artsch-wager, *Jour. Agr. Res.*)

The relative activity of the tissues which enter into the development of the tuber may be indicated in the following order; the initial activity occurs in the pith and cortex, but the perimedullary zone is the most active region and produces the largest proportion of the tissue of the mature tuber. The parenchyma of the outer phloem is relatively inactive, but divisions take place so that this zone keeps pace with the enlargement of the tuber without greatly increasing its width. The cambium, contrary to the



SOLANUM TUBEROSUM

interpretation of de Vries, is relatively inactive and produces little secondary tissue.

THE ONTOGENY OF THE TUBER. — Following the elongation of the rhizome, which normally reaches a length of 3 to 4 inches, the first change incident to tuber formation is the radial enlargement of its tip. The first region to grow actively is the pith; and, as a result of its increasing size, the elements of the vascular cylinder are inclined obliquely outward from the course which they follow in the axis of the rhizome.

To compensate for medullary growth, tangential enlargement and radial divisions of cells take place simultaneously in the cortical, perimedullary, and vascular regions. As tuberization proceeds, the cortical cells become filled with starch and the storage character of the organ is definitely indicated. Following cell division in the pith and the coincident compensating growth in the cortex, the pericyclic and perimedullary zones become the regions of greatest growth activity. The pericyclic cells surrounding the outer groups of primary phloem divide, enlarge rapidly, and, like the cells of the cortex, become filled with starch. They appear to be in direct contact with the cortical parenchyma and also form radial wedges of tissue between the outer phloem groups.

In early ontogeny, the endodermis does constitute a line of demarcation between cortex and outer pericyclic zone and this helps to eliminate the possibility of misinterpreting the outer pericyclic storage region as a centripetal extension of the cortical parenchyma. (Fig. 285, B, C.) The failure of the endodermis to form Caspary strips as the girth of the stele increases finally results in its disappearance as a distinct layer. The activity of the pericycle causes the original groups of outer phloem to become widely separated, and additional ones are formed in the intervening areas which consist of a few sieve tubes, companion cells, and parenchyma.

Changes similar to those taking place in the pericycle occur in the inner pericyclic and perimedullary zone, where rapid and continuous cell division results in the spreading and centripetal deflection of the inner phloem groups. There is a limited amount of cell division in the vascular ring which causes a tangential dispersion of the xylem elements and a radial separation of the protoxylem from the metaxylem. (Fig. 285, A.) The epidermis of the tuber primordium is ephemeral because of the activity of

these zones in tuberization; but, for a short time, anticlinal walls are laid down in some of the epidermal cells to compensate for the increasing size of the tuber. This is followed by periclinal divisions so that the initial periderm may be of epidermal origin rather than hypodermal as indicated by Reed (18).

While the epidermal cells are dividing periclinally, the hypodermal layer begins to function as a phellogen, and tangential divisions produce a periderm that is from six to fifteen layers in width. The initial activity of the phellogen begins at the stem

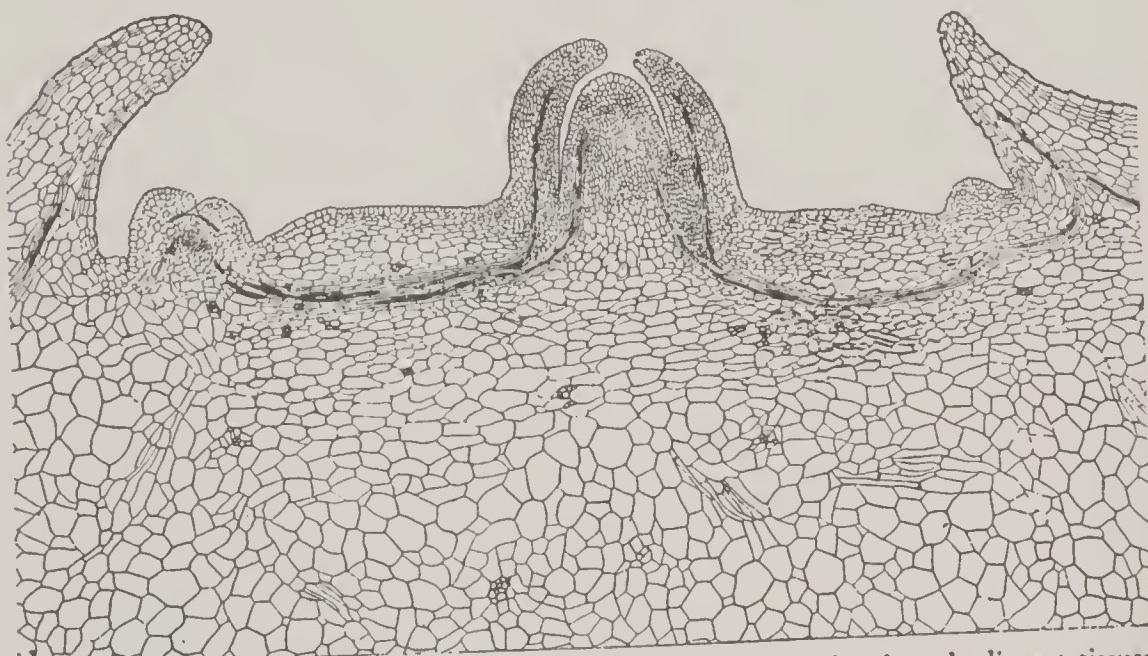


FIG. 287. Longisection through tip of tuber showing structure of buds and adjacent tissues.
(After Artschwager, *Jour. Agr. Res.*)

end; and by the time the tuber is the size of a pea, it has extended over the entire tuber. The phellogen remains active throughout the growth of the tuber and new phellem cells are formed to replace those that disintegrate as a result of its enlargement. The individual cork cells are brick-shaped with thin suberized walls and form a compact layer without intercellular spaces. At maturity they are devoid of contents, although in some varieties they may contain pigments similar to those found in the peripheral cells of the cortex. Coincident with the formation of the periderm, the cells which underlie the stomata begin active division and produce loose masses of rounded cells. Under favorable conditions, these rupture the epidermis and proliferate, forming small white dots, lenticels, on the surface of the tuber. During tuberization, the buds or "eyes" are differentiated in the axils

of the small scale leaves which occur in the same phyllotaxy as the foliage leaves. Each "eye" may contain three or more buds. (Fig. 287.) As the tuber enlarges, new buds are formed at its apex, and the older ones develop to maturity, establishing vascular connections with the stele.

ONTOGENY OF THE LEAF. — The development of the leaf has been described by de Vries (26) and Artschwager (1).

The leaf primordia arise from the growing point of the stem as small protuberances which elongate and curve adaxially so that they finally arch over the growing point. While this growth and curvature are taking place, the primordia undergo form changes, the first being the production of lateral projections on both sides of the primordium that later become the blades of the terminal leaflets. Very early in ontogeny, the terminal leaflet consists of a short stalk and blade with a well-developed midrib, and the halves of the lamina are folded so that their adaxial faces oppose each other. For some time, the terminal leaflet is far advanced in its development over the other leaflets which differentiate gradually, and the slow elongation of the axis of the leaf provides space for the formation of the primordia of the lateral leaflets. Artschwager (1) states that "the difference in the rate of development is so great that the terminal leaflet is already one centimeter in length and has become green long before the rest of the leaflets appear." The development of the lateral leaflets occurs in basipetal succession and the uppermost leaflets are green and well developed when the lower ones are still primordia.

The first epidermal hairs appear early on the abaxial surface of the primordium, developing acropetally; and, later, hairs are produced on the adaxial surface in the same order. These arise in longitudinal rows adjacent to the veins, and the first glandular ones are soon followed by hairs that are stiff and unicellular. Both kinds increase in number rapidly and mature before the mesophyll is completely differentiated. While the leaf is small, the hairs form a dense mat over the veins; but, since no new hairs are formed, the density decreases as the leaf enlarges and they are widely scattered at maturity.

In the development of the mesophyll, the cells adjacent to the upper epidermis elongate to twice their original height and form a compact palisade region; while the remaining parenchymatous cells comprising the spongy region are approximately isodiametric.

In the mature blade, there is one layer of palisade cells and three to five rows of spongy tissue. (Fig. 288, A.)

Differentiation of the vascular system is not completed until the blade is fully developed. It is similar in general details to that of the stem except for the position, number, and size of the vascular elements. In the leaf primordium small crescentic groups

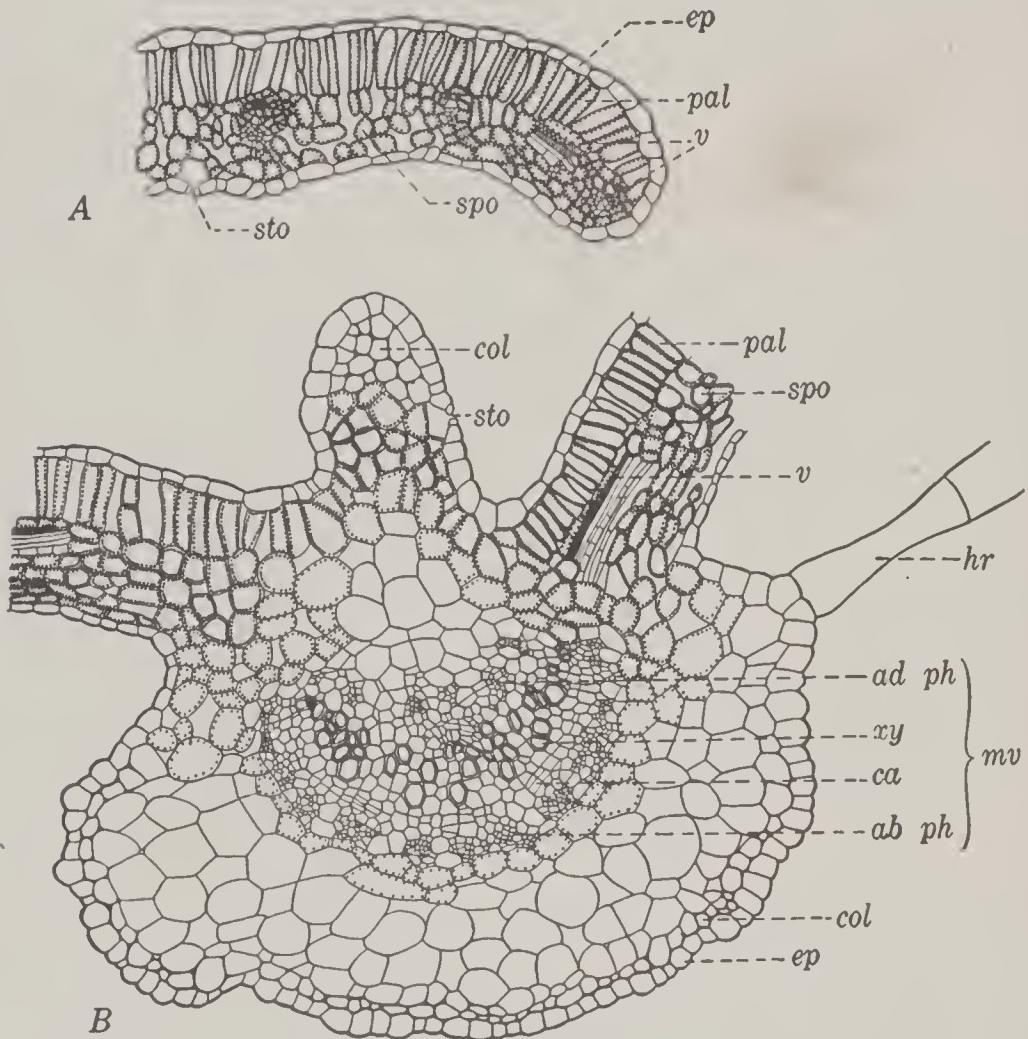


FIG. 288. A, transection of margin of leaflet showing mesophyll and small veins; B, transection through midvein of leaflet: *ab ph*, abaxial phloem; *ad ph*, adaxial phloem; *ca*, cambium; *col*, collenchyma; *ep*, epidermis; *hr*, hair; *mv*, midvein; *pal*, palisade; *spo*, spongy tissue; *sto*, stoma; *v*, lateral vein; *xy*, xylem.

of procambial cells occur, surrounded by the larger cells of the fundamental parenchyma; and, at about the center of each group, a few protoxylem elements are differentiated. This is followed by the appearance of phloem initials which form a band of smaller cells at the periphery of the procambial strand. The adaxial (inner) phloem is the first to be differentiated, and these groups, though few in number, make up the larger portion of the phloem

tissue. The abaxial (outer) phloem forms a nearly continuous band on the abaxial side of the procambium.

As the leaf matures, the cells of the procambial strand lying between the abaxial phloem and the primary xylem form a cambium which later gives rise to secondary vascular elements. (Fig. 288, B.) In the mature leaf, both the abaxial and adaxial phloem groups are distinct; but, in the principal veins, these may be continuous around the flanks so that the bundle is essentially amphicribral. The lateral veins resemble the midvein, but the size and number of the phloem groups gradually decrease in the smaller ones. No adaxial phloem is differentiated in the terminal veinlets, which consist of one or two spiral protoxylem elements and some adjacent conducting parenchyma located on the abaxial side of the protoxylem.

DEVELOPMENT AND VASCULAR ANATOMY OF THE FLOWER. — Floral development has been studied in several genera of the Solanaceae and appears to be uniform for the family. The reports of Young (31) for *Solanum*, Augustin (3) on *Capsicum*, and Warner (27) for *Lycopersicum* are in general agreement. The flower cluster is terminal, although it appears lateral in the later stages of its development owing to the growth of the adjacent axillary bud which forms the continuation of the vegetative axis of the plant. The primordium of the flower appears as a dome-shaped enlargement which at first is directly in line with the main axis, and its parts develop in acropetal succession. The ensuing details of development are similar to those described for *Lycopersicum*. (Chapter XVIII.)

In the pedicel of the flower the vascular tissue constitutes a more or less continuous region; but as it broadens to form the receptacle of the flower, five vascular strands diverge from this cylinder and incline outwardly to occupy a peripheral position. These form the five principal traces of the sepals. Slightly above this point of divergence the parenchymatous gaps formed by them are closed and the vascular cylinder again appears to be continuous. This is followed by the divergence of five bundles constituting the traces to the petals that alternate with the traces to the sepals. At this same level, divisions of the original sepal bundles result in the formation of lateral bundles so that each sepal has from three to five vascular strands. The same situation prevails in connection with the bundles to the corolla, and each petalulti-

mately is supplied by one large median and four lateral bundles. Above the point of departure of the traces to the petals, five staminal traces diverge that alternate with those of the petals and are opposite the main traces of the sepals.

Above the level at which the stamen traces diverge, the vascular system is more or less elliptical in transection; and, at each end of the ellipse, a small bundle passes outward and upward, one opposite a petal and the other opposite a stamen. These are the abaxial carpillary bundles which extend into the style for a distance nearly equal to its length. The main vascular tissue again becomes continuous, closing the gaps so that the stele appears in transection as two crescentic masses broken by traces extending outward and upward through the lateral walls of the carpels. At a higher level, the vascular cylinder is divided into many small bundles, some anastomosing to form a vascular network while others extend into the ovules. Thus the vascular supply to the ovules is apparently cauline rather than foliar.

FLORAL ABSCISSION. — Some varieties habitually produce more flowers than others; but in any given variety, flower production may be extremely variable from year to year. The formation of flowers does not necessarily mean that development will continue to the point where the fruits or "seed balls" are produced containing viable seed, and it commonly happens that abscission of the flower may occur at some stage prior to the maturation of the fruit and seed. Dorsey (10) has investigated this matter, and reports that the abscission of the flowers bears no essential relation to abortion of pollen or failure to receive a stimulation from pollination and fertilization. He regards abscission as being due to "physiological influences operating independently of pollen or pistil development."

Young (29) has described the shedding of the blossoms in some detail and points out that the abscission occurs at a definite point about half an inch below the base of the blossom where there is a joint in the pedicel of the flower. It is at this point that the abscission layer is formed. This is marked at a very early stage by a constriction in the pedicel beneath which the cells are smaller than in the tissues immediately above or below. These cells have dense protoplasmic contents with large nuclei, and form a meristematic zone that is capable of growth and cell division after the adjacent cells have become inactive. The abscission

layer at first extends across the stem in a transverse direction; but, later, the plane of the layer is curved downward, and the stem becomes swollen below the constriction owing to the multiplication of the cells in the cortex.

No definite line of cleavage is formed before the shedding of the flowers, nor is a true cork developed prior to that time. As long as the blossoms appear to develop normally, the cells of the abscission layer remain firmly joined; but, when blasting and yellowing of the buds or blossoms occurs, a cleavage results in the upper portion of the abscission region. The active tissue on the pedicel then forms a callus over the broken surface. Abscission may take place at any stage in the development of the buds or blossoms.

MICROSPOROGENESIS. — The sporogenous tissue is differentiated early in the development of the anther, and may first be recognized as a mass of small dense cells with large nuclei which occupy each of the four lobes of the anther. The archesporium consists of a layer about two cells in thickness which is parallel to the surface of the anther. It is covered by the epidermis and a variable number of layers of parietal cells. The tissue of the archesporium extends back the entire length of the anther, appearing in cross section as a horseshoe-shaped structure. Since the liberation of the pollen is through terminal pores, there is no modification of the parietal cells to aid in dehiscence. The tapetal cells are large but as the pollen grains mature the entire tapetum and the inner parietal layers become disorganized. The archesporial cells divide several times and the daughter cells are more or less angular in shape. Finally, they lose their angularity and function as microspore mother cells, producing the microspores as a result of two successive divisions, the first of which is heterotypic.

Rees-Leonard (19) has observed several types of degeneration during the floral development and sporogenesis of the potato. A common type occurs in microsporogenesis in which the sporogenous tissue completely disintegrates; and in some of the ovules of such buds, the development of the megasporangium seems to be arrested. Degeneration may occur within the ovule at any stage in development, but is less frequent in very early ones. In some cases, it takes place following the meiotic divisions and all four megasporangia disintegrate; while, in others, the degeneration occurs during the development of the megagametophyte. This

may happen during the early stages, or following the formation of the eight-nucleate gametophyte. In commenting upon these occurrences, Rees-Leonard states,

"These irregularities which occur during macrosporogenesis and the development and maturation of the macrogametophyte may partially account for the failure of seed and fruit development in the potato. There seems to be some correlation, however, between the irregularities occurring during microsporogenesis and the development of the pollen grains on the one hand, and those taking place during macrosporogenesis and macrogametophyte development in the ovules of the same flower on the other hand."

MEGASPOROGENESIS AND THE MEGAGAMETOPHYTE. — The formation of the partially campylotropous ovules from the massive cauliné placenta has been described in connection with the development and structure of the seed. At the time that the ovules first become slightly inclined the archesporial cell differentiates in the hypodermis just over the bent tip of the ovule; and, according to Bhaduri (5), this occurs prior to the differentiation of the integument. The archesporial cell, which is larger than the adjacent cells of the hypodermis, functions directly as a megasporangium. It enlarges and becomes somewhat vacuolate prior to the two successive divisions which result in the formation of a linear tetrad of megaspores, each of which is invested with a distinct cell wall. When first formed, the megaspores are alike in size and content; but soon the one at the chalazal end of the nucellus begins to enlarge and there is a gradual degeneration of the other three, beginning at the micropylar end. The three disintegrated megaspores form a cap over the functional one which by its growth compresses the others into a compact mass.

In the development of the megagametophyte from the functional megasporangium, the two-, four-, and eight-nucleate stages occur in rapid succession. The synergids and megagamete are located toward the micropyle, and the position of the antipodals and development of the fusion nucleus follow the common program found in most angiosperms. The megagametophyte is surrounded by a thin nucellar layer; but, at maturity, these cells degenerate completely so that the fully developed gametophyte lies appressed to the innermost layer of the integument.

Variations in the development of the gametophyte have been reported in this family. Nanetti (16) and Young (31), investigat-

ing *Solanum muricatum* and *Solanum tuberosum* respectively, have described the development of the gametophyte as being similar to what was once called the "Lilium" type of development in which all four megasporangia remain functional and divide to produce the eight-nucleate gametophyte. Studies by Bhaduri (5), Cooper (8), and Schnarf (21) indicate that the Solanaceae have the usual angiospermous type of gametogenesis.

According to Bhaduri and Souèges (22) the presence of tapetal tissue covering the embryo sac is a characteristic feature of the Solanaceae, and the former found that it was derived from the

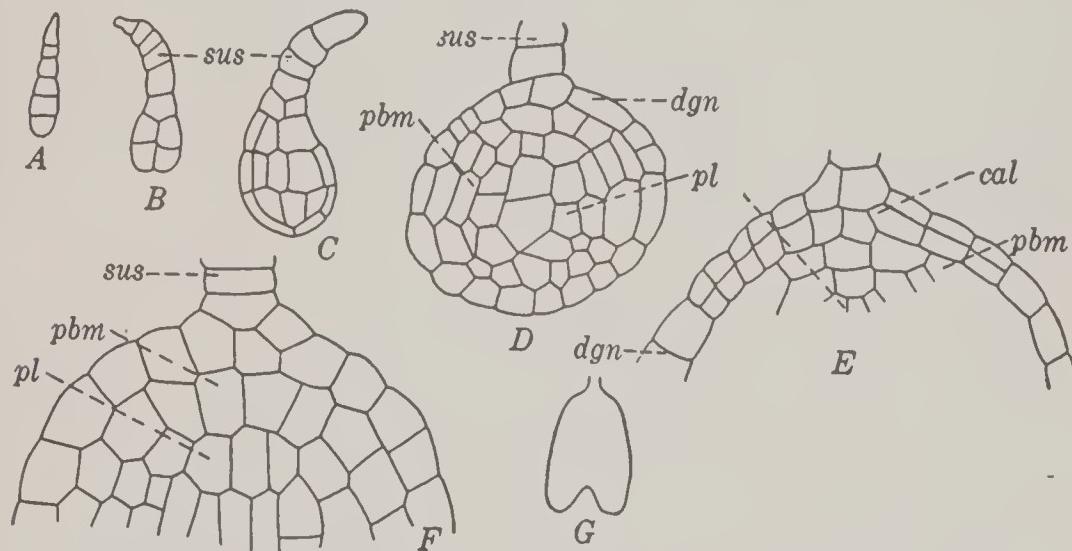


FIG. 289. A-F, stages in development of embryo; G, diagrammatic outline of young embryo at time of differentiation of cotyledons: *cal*, calyptrogen; *dgn*, dermatogen; *pbm*, periblem; *pl*, plerome; *sus*, suspensor. (After Tognini, *Ist. Bot. Univ. Pavia*.)

integument in all species investigated. This tissue serves the dual function of secretion and absorption.

Young (30) has reported three instances in which the ovule contained two megagametophytes. In these cases, the vascular strands supplying the ovule branched in the funiculus and a branch was directed toward each gametophyte.

EMBRYOGENY. — Embryogeny in the Solanaceae has been studied by several investigators including Guignard (14), Souèges (23), Tognini (25), Ferguson (13), and Bhaduri (6). Guignard reports that there is no early, free-nucleate stage in the formation of the endosperm and describes double fertilization in the case of *Nicotiana* and *Datura* with endosperm formation following triple fusion. Ferguson, while agreeing with Guignard in respect to the absence of a free nucleate stage, has demonstrated in *Petunia* that the first divisions of the fusion nucleus occur prior to fertilization.

Following fertilization, the zygote undergoes a series of transverse divisions which result in the formation of a linear series of cells. (Fig. 289, A.) The basal cells of the proembryo form the suspensor, and vertical divisions of the terminal cells result in the development of an enlarged spherical structure which becomes the embryo. Early in its differentiation, there is a blocking off of definite histogens so that the initials of the dermatogen, the periblem, and the plerome can be determined; and development of the epidermis, cortex, and stelar structures then follows. (Fig. 289, D, E, F.) The embryo soon becomes bilobed; and subsequent growth of these lobes leads to the formation of the two cotyledons, while elongation and differentiation of the axis of the embryo result in the production of the hypocotyl and radicle. (Fig. 289, G.) During ontogeny, the endosperm develops rapidly and at maturity it completely surrounds the embryo. (Fig. 275, A.)

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CHAPTER XVIII

SOLANACEAE — *Continued*

LYCOPERSICUM ESCULENTUM

THE tomato is a native of South and Central America and probably had been cultivated there by the native population long before its introduction into southern Europe. It attained great favor there and was introduced into the United States in the latter part of the eighteenth century. At present, it is grown extensively throughout the United States for home, market-garden, and canning purposes. In addition to its commercial uses, the tomato plant might be regarded as the "guinea pig" of the plant kingdom, since it has been widely used for experimental purposes in problems of plant physiology, pathology, and genetics, owing to the ease with which it may be propagated, and its hardiness and adaptability to a wide range of environmental conditions.

Bailey (2) recognizes two species, *Lycopersicum esculentum* Mill., and *L. pimpinellifolium* Dunal; but the latter, known as the currant tomato, is not widely used. It has a spreading habit, small leaves, flowers arranged in long racemes, and a small two-loculed berry about $\frac{3}{8}$ to $\frac{1}{2}$ inch in diameter. Five botanical varieties of *L. esculentum* are listed by Bailey (3), and there is a large number of commercial varieties. Boswell and others (4), in cooperation with members of the seed trade, canners, and market-gardeners, have described the nine most widely used American varieties in an attempt to eliminate some of the confusion that exists with respect to their characteristics. They point out that the vegetative habit is so variable and susceptible to modification on the basis of response to environmental conditions that it is difficult to give an exact description of any of the leading varieties in terms of actual measurements. For this reason, the following account is a generalized one designed to present the characters that are important in connection with structural and anatomical studies rather than to describe the specific characteristics of any commercial type.

GENERAL MORPHOLOGY

The tomato plant is grown in the United States as an annual, and the length of time required for maturation of the fruit, after transplanting into the field, ranges from 55 to 65 days for rapidly maturing varieties, and from 85 to 100 days for the slowly growing canning types grown in northern and central California. The latter may not attain the peak of the harvest until 100 to 125 days after transplanting. The variation in the size of the plant is equally striking. In general, early varieties are small in stature (16 to 18 inches in height) with a maximum spread of 4 to 4½ feet, while the slowly maturing forms are much larger, attaining a height of 24 to 28 inches and a maximum spread of 6 or 7 feet. These figures refer to plants which have been grown without pruning.

THE ROOT. — The character of the root system is greatly modified by cultural practices. When grown from seed, without transplanting, a strong tap root is formed which, according to Weaver and Bruner (36), may grow at a rate of an inch a day attaining a depth of nearly 2 feet. In actual practice, the plants are started in seed beds and transplanted once or twice before being set in the field so that the primary root is injured and a dense fibrous system of lateral and adventitious roots is formed. After the final transplantation to the field, the adventitious roots develop rapidly and, in mature plants, may have a lateral spread of 5 feet, with numerous large branches. These occasionally penetrate 3 to 5 feet, although the major portion of the root system occupies the first 8 or 10 inches of soil.

THE SHOOT. — The growth habit varies from the spreading vine type through forms that are semi-erect to erect. (Fig. 290.) In decumbent forms, there are relatively few short branches which attain a length of 2 to 2½ feet and a diameter of approximately an inch at the base. In large erect types, the main stems are very thick, reaching a diameter of an inch and half, and the branches, which range from 10 to 17 in number, may be 6 feet in length. The branching is usually sympodial so that the successive principal axes are developed from axillary buds and the terminal buds produce inflorescences or abortive branches. (Fig. 291.) Each axillary bud continues the vegetative shoot, producing leaves at several nodes, and then terminates in an inflorescence. This mode of development may be repeated many times until the axis is several

feet long, bearing inflorescences and fruits throughout its length. At the base of the plant and where no inflorescences are developed, the branching may be monopodial. A case of true dichotomy of



FIG. 290. The tomato plant in fruit, variety Marglobe. (Courtesy of the Ferry-Morse Seed Co.)

the vegetative axis has been reported by Caldwell (6) but this is not common except in the dichotomous branching of some inflorescences.

Adventitious roots develop readily from the stems, and for this reason propagation by means of cuttings is sometimes practiced in

greenhouse culture. This is especially helpful in experimental work of a genetic character, such as that carried on by Lindstrom and Koos (21), where it is essential to perpetuate the plant without modification of the genetic pattern. They were able to propagate for five years without mutation or change a haploid (12 chromosomes) tomato plant which arose spontaneously in an F_2 generation.

The arrangement of the leaves is usually alternate with a $\frac{2}{5}$ phyllotaxy. They are odd-pinnately compound, the number of



FIG. 291. The plant showing sympodial branching.

larger leaflets ranging from seven to nine, rarely eleven; and, between the adjacent pairs of major leaflets, a variable number of smaller ones occur. In the smaller varieties, there may be from four to six intermediate leaflets, and as many as nine to eleven occur in the larger, more vigorously growing types. The margins of the leaflets are variously incised or lobed except in *Lycopersicum esculentum*, var. *grandifolium*, in which they are entire. Capitate glandular hairs and large pointed non-glandular ones occur as on the stem. (Fig. 292, E.)

The short petioles are relatively constant in length, ranging from $1\frac{1}{4}$ to $2\frac{1}{2}$ inches, and the compound blade is approximately as

wide as long. The length in the early varieties ranges from $6\frac{1}{2}$ to $8\frac{1}{2}$ inches, while in the larger types it may be slightly in excess of 12 inches. In general, the leaf characters alone are of little diagnostic value in separating the commercial varieties, as the leaves exhibit great differences owing to variation in climate, soil conditions, and cultural methods.

THE INFLORESCENCE. — The inflorescence is usually a two-ranked raceme or a branched racemose-cyme, the former type

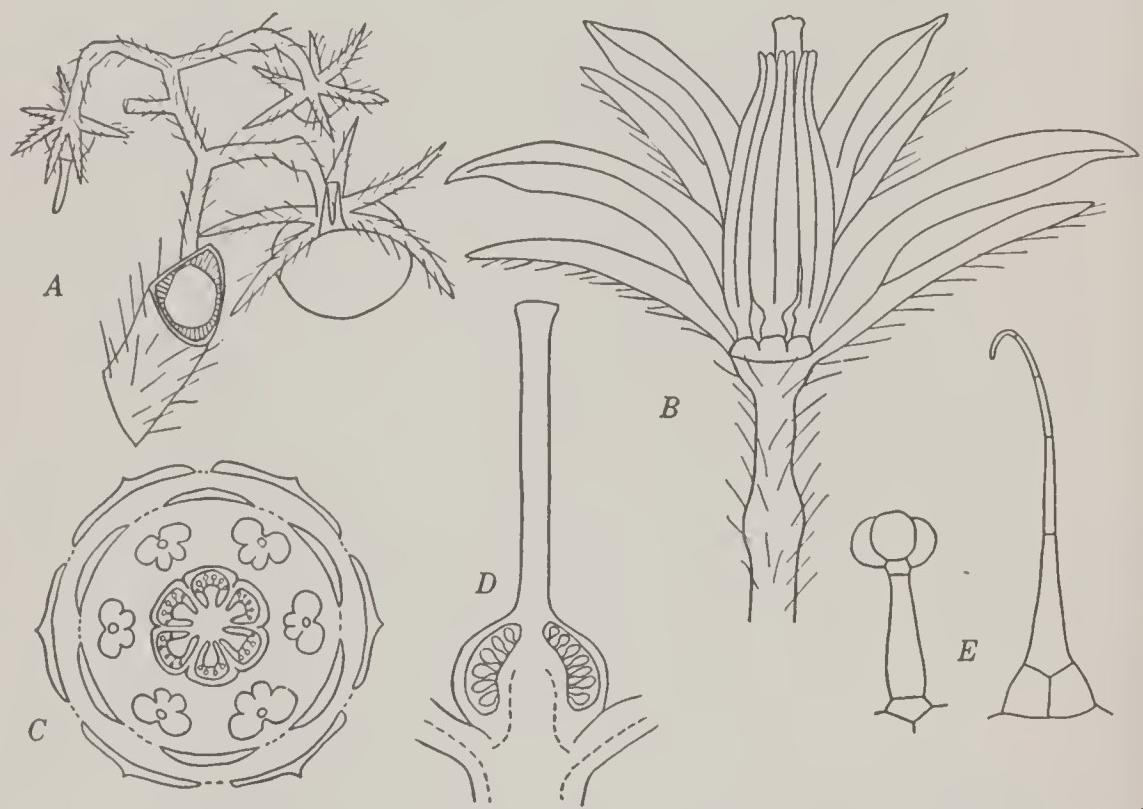


FIG. 292. *A*, inflorescence showing unequal development of fruits, one flower has abscised; *B*, flower with portion of perianth removed showing relation of stamens and pistil; *C*, floral diagram of hexamerous flower of Stone variety; *D*, longisection of pistil with caulin placentation; *E*, two types of hairs commonly found on calyx, pedicel, and vegetative parts.

occurring only in the currant tomato. (Fig. 292, *A*.) Bouquet (5) made a study of the inflorescences of several varieties in order to determine their characteristics and the fruiting habit in each instance under greenhouse conditions. He described three types of inflorescence, which sometimes occur on the same plant: (1) simple raceme; (2) dichotomous or two-forked flower clusters; and (3) the polychotomous inflorescence having more than two forks or branches. The simple type occurs more frequently on the lower portion of the plant, and the branched types are more common on the upper parts.

The number of flowers comprising an inflorescence may vary from four to twelve or more. Boswell and his coworkers (4) found that the more important commercial varieties bear an average of four to five flowers per cluster; and that, under conditions where the plants are not pruned or staked, from two to four flowers set fruit. Ordinarily, it is unusual for more than two flowers of an inflorescence to be open at one time; and, because of this progressive development, a single raceme may have small fruits, open flowers, and buds. Under greenhouse conditions, some unproductive flowers occur. These may be classified into three categories: (1) those producing small fruits that ripen prematurely before attaining a marketable size; (2) those having a persistent calyx, but in which the fruit does not develop; and (3) flowers that absciss.

FLORAL ABSCISSION. — Kendall (17) has described the histology of the pedicel of the flower and fruit with reference to the development of the separation zone, the process of abscission, the time involved, and experimental methods of inducing abscission. The zone of separation in *Lycopersicum* is located at a mid-point in the pedicel in contrast to *Nicotiana* where it occurs at the base. It is externally visible because of enlargement at that point and owing to the development of a circumferential groove which is fully half the depth of the cortex. (Fig. 292, A, and Fig. 293, A.)

The vascular system of the pedicel forms a cylinder of separate bundles which are surrounded by parenchyma. Outside the fundamental parenchyma, there is a layer of collenchymatous cells in that portion of the pedicel which is proximal to the groove, but this does not develop in the portion distal to it. Between the collenchyma and the epidermis there is a zone of chlorenchyma. (Fig. 293, B.) The separation layer consists of from three to six tiers of cells which are located in the plane of the groove. In buds in which the calyx is less than 2 mm. long, the groove is not detectable, but it begins to appear when the corolla is about 1 mm. in length, and is well developed in young buds in which the corolla does not exceed 3 mm. The cells of the separation zone are smaller than those on either side of it, and this difference in size becomes more noticeable as the flowers mature, since the cells of this region do not enlarge as the adjacent cortical cells increase in size. There are apparently few cell divisions in the separation zone, but the cells do retain their meristematic potentialities. The mechanical

tissues of the pedicel are not continuous through the separation layer as in *Nicotiana* so that there is a break in a plane parallel to the bottom of the groove. It is possible, therefore, for abscission to cause the fall of the fruit at any stage in its development,

but this rarely occurs except at about two or three days after anthesis.

On the basis of his investigation, Kendall agrees with Kubart (20) that the separation layer represents "merely a portion of the primary meristem which retains its original physiological capacities." During the development of the fruit, there is a very definite increase in the size of the pedicel which is restricted almost entirely to the portion distal to the groove; and its diameter in the fruit may be two or three times greater than at the time of the anthesis of the flower. This results from the enlargement and division of the cells of the cortex, and the diameter of the pith remains practically constant.

Abscission involves the separation and isolation of the cells in the separation zone. Frequently, the

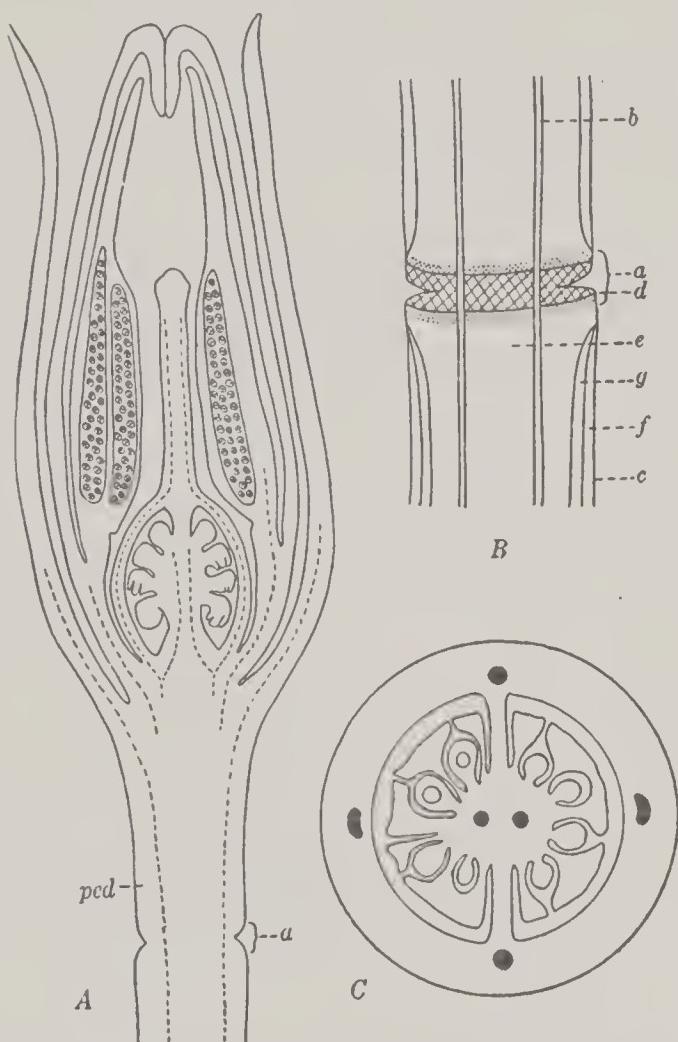


FIG. 293. A, diagrammatic longisection of young flower just prior to anthesis, showing development of caulinovous ovules and location of abscission layer; B, diagrammatic longisection of portion of pedicel in which abscission zone is located; C, transection of ovary of bicarpellate pistil showing fleshy central placentae which have grown around and embedded developing ovules: *a*, abscission zone; *b*, vascular strands; *c*, epidermis; *d*, separation layer; *e*, pith; *f*, chlorenchyma; *g*, collenchyma; *PED*, pedicel. (B, redrawn after Kendall, Univ. of Calif. Pub.)

process is initiated in the pith as well as the cortex, and proceeds independently in the two regions until the final break occurs through the vascular tissue and the epidermis. The separation begins in two tiers of cells at the bottom of the groove, but may later affect three or four layers. It takes place in such a way

that the separation surface of the detached portion of the pedicel may be convex, while that of the remaining part of the pedicel is slightly concave.

The separation of the adjacent cells results from a dissolution of the middle lamellae, and on the basis of Kendall's experiments, it seems probable that turgor is not an initiating factor, but serves mechanically to hasten the process. It appears from this work that the middle lamellae of the cell walls in the abscission zone are more easily hydrolyzed than are those in the more distal portions, and the agent of hydrolysis is thought to be an enzyme. No cell divisions or elongations were observed accompanying the process of abscission.

In addition to this type of true abscission, individual plants may lose their flowers by a process which involves no active cell separation. In such cases, the flower merely wilts and dries back to the abscission groove, where it may hang until broken off by some mechanical means. When this type of abscission occurs, it is first indicated by a loss of chlorophyll in the pedicel, beginning at the tip and extending to the separation zone. In many instances, both types of abscission may occur in the same plant.

THE FLOWER. — The pendent yellow flowers are perfect, hypogynous, and regular; but in cultivated varieties, the number of floral parts in each cycle is variable. The persistent calyx consists of a very short tube terminated by five to ten lobes. The rotate corolla also has a short tube which is expanded at the top into five or more lobes that are at first greenish-yellow, becoming a brilliant yellow later when the flower is fully developed and the lobes reflexed. The five or more stamens are partially adnate or undiverged from the calyx tube. The filaments are short and the connivent anthers are united laterally to form a hollow cone around the pistil. The pistil consists of two to several carpels and its elongated style and smooth, flattened stigma extend through and somewhat beyond the encircling androecium. (Fig. 292, B.)

The solanaceous plants are usually pentamerous and the basic floral plan is 5-5-5-2. Warner (35) has described the ontogeny of a flower of this type, while Cooper (7) and Smith (27) have published accounts of the development of the hexamerous form which is the most common floral plan in many commercial varieties. (Fig. 292, C.) In fact, Cooper found only one pentamerous blossom in more than a thousand flowers examined. In addition to *L. esculentum*,

lentum, var. *cerasiforme*, the type investigated by Warner, the form *L. esculentum*, var. *pyriforme*, is also pentamerous with a bilocular ovary.

ANATOMY

ONTOGENY OF THE FLOWER. — The floral primordium first appears as a dome-shaped enlargement which is directly continuous with the main axis, and its parts develop in acropetal succession.

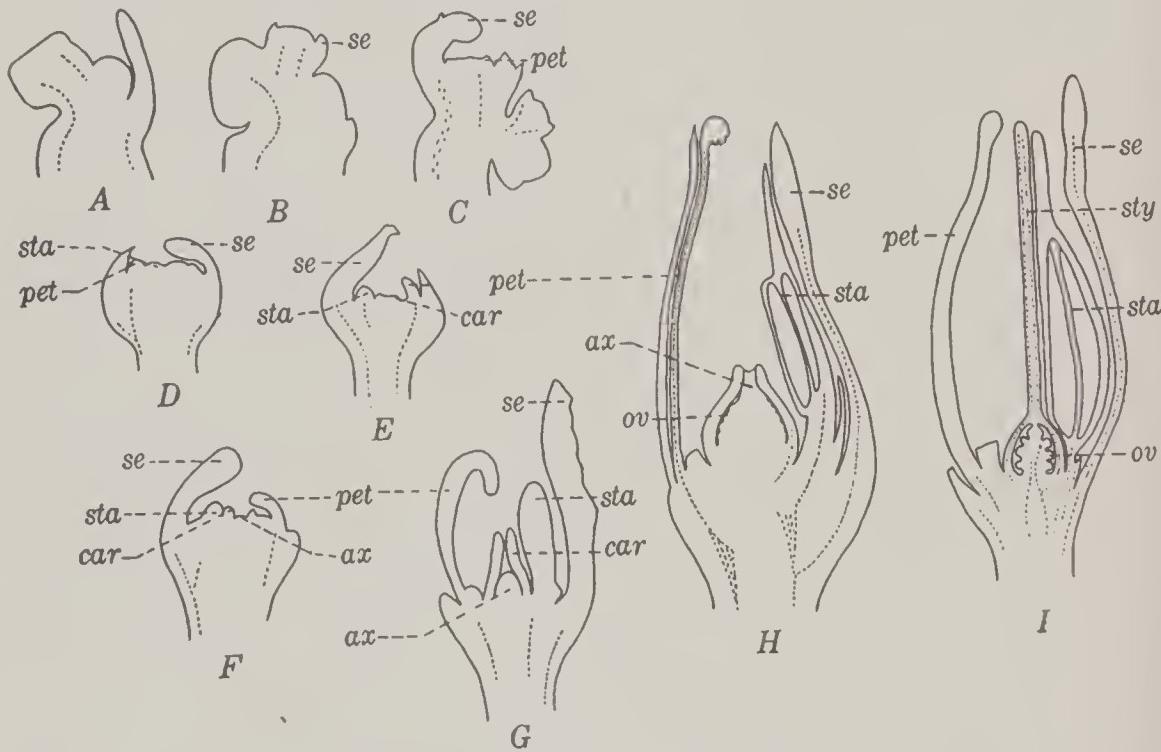


FIG. 294. *A-I*, stages in floral development: *B*, stage showing origin of sepal primordia; *C*, more advanced stage showing primordia of sepals and petals; *D*, origin of stamen primordia; *E*, origin of carpel primordia; *F*, *G*, and *H*, longisections of flower buds showing advanced stages in development of stem axis in relation to carpels; *I*, longisection showing united carpels and development of style: *ax*, stem axis; *car*, carpel primordium; *ov*, ovule; *pet*, petal primordium; *se*, sepal primordium; *sta*, stamen primordium; *sty*, style. (Redrawn after Warner.)

(Fig. 294, *A*) Peripheral enlargement and rapid cell division of this protuberance result in the formation of a somewhat raised blunt ridge at the margin of the primordium. This is followed by accelerated growth on the ridge at five or more equidistant points, and the resultant outgrowths constitute the sepal primordia. (Fig. 294, *B*.) These arise in a clockwise direction; and by the time the cycle is complete, the first sepal lobe is somewhat advanced. The growth of the sepal primordia is more rapid on their abaxial sides so that the free tips incline toward each other as they elongate and partially enclose the cavity beneath them.

After this overarching has been accomplished, there is little further individual growth; but the entire basal portion of the calyx ring grows uniformly to form a short cylindrical calyx tube. Each sepal has three to five bundles with fine branches that extend throughout all parts of the lobe. The structure of the calyx lobe is leaf-like and the mesophyll consists of about fifteen layers of spongy parenchyma. The epidermis is covered by a thin cuticle; and numerous stomata occur on the abaxial surface, especially on the tube and at the base of each lobe. The guard cells on the abaxial surface protrude somewhat above the other epidermal cells, while the smaller ones on the adaxial surface are not raised. The calyx is pubescent, producing short, unicellular hairs and longer multicellular ones with a group of basal cells. The glandular hairs are stalked and terminated by a group of four or more cells. (Fig. 292, E.) Short-stalked hairs and papillae occur on the adaxial surface of the calyx lobes.

Following the differentiation of the sepals, the continuous circular ridge of the corolla develops from the growing point of the flower primordium centrad to the sepals. On this, the primordia of the petal lobes arise at points alternate with those of the calyx, and their growth results in the formation of the five or more distinct triangular teeth of the gamopetalous corolla. (Fig. 292, C.) Just prior to anthesis, the corolla grows rapidly and pushes the calyx open. (Fig. 293, A.) The epidermis of the corolla is composed of thin-walled cells; and on the adaxial surface near the apex of the lobes, many of them protrude as papillae. Numerous glandular hairs with short stalks occur on the abaxial surface. Stomata are lacking. The corolla lobes are about eight to ten layers in thickness and yellow chromoplasts occur in the spongy mesophyll.

The stamen primordia arise as the corolla elongates and its undiverged base becomes tubular. They are alternate with the lobes of the petals, and are diverged near the base of the ridge from which the petal primordia are developed. (Fig. 294, D.) This is followed by the growth of the zone basal to the stamens and petals, so that the lower portions of the filaments appear to be undiverged from the tube of the corolla. (Fig. 293, A.) The terminal portion of each stamen primordium develops independently and at first they are distinct; but, later in ontogeny, the anthers may be somewhat closely appressed laterally. The anther

is bilobed, the lobes being separated by connective tissue; and each one develops two microsporangia which extend its full length. The abaxial surface of the anther is papillate, while the adaxial one has few hairs. No stomata are present.

In the bicarpellate types, the carpillary primordia arise soon after the differentiation of the stamens. They appear centrad to the joint petal-stamen zone, and are so arranged that one carpel is opposite a stamen, the other being alternate with two stamens. (Fig. 294, *E*, *F*.) In hexamerous forms, the six-carpillary primordia are alternate with the stamens. (Fig. 292, *C*.) The early development of the two carpels results in the formation of conical hood-like structures whose concave faces oppose each other. Within the carpel primordia, there remains a definite portion of the axis which consists of a more or less flat or concave disk. This part of the axis begins to elongate, and enlarges to form a conical structure. (Fig. 294, *G*.) Later, growth is initiated at the base of the elongating cone; and two septa develop involving a portion of the axis and forming two locules. At this time, each carpel is open at the top; and its cavity is a pit bordered by the elongated central portion of the axis, the ridge-like septa, and the curved walls of the carpel. (Fig. 294, *H*.) Continued growth of the carpels results in the tip of each being inclined toward the central portion of the axis, and finally they become so closely appressed to the elongated column of the axis that the two structures are no longer recognizable as distinct from each other. Further elongation of the terminal portions of the carpels results in the formation of a long narrow style. Continued enlargement and a bowing out of the basal wall of each carpel forms two locules in which the central axis develops as a columnar structure from which the ovules arise. (Fig. 292, *D*, and Fig. 294, *I*.)

Although the placental structure is at this stage continuous with the carpillary tissue, it is largely caulin in origin; and the ovules may be regarded as arising from caulin, axile placentae rather than from foliar ones. (Fig. 293, *C*.) The epidermal cells of the ovary as well as of the basal portion of the style are papillate; and multicellular, glandular, and non-glandular hairs are also produced. Cooper (7) observed a few large stomata in the stylar epidermis, but found none in the epidermis of the ovary, agreeing in this regard with Groth (11), Rosenbaum and Sando (26), and Gardner (10). Both Gardner and Cooper reported stomata on the

pedicel, receptacle, calyx, and style; and Makemson (24) found stomata and lenticels on the ovary.

MICROSPOROGENESIS.—According to Smith (27) sporogenous tissue develops early in the anthers, and a row of hypodermal archesporial cells are differentiated in very young buds. Inside the archesporial cells, a single row of primary sporogenous cells is formed and these continue to divide. The outside row becomes the outer tapetum; while, early in development, the vegetative cells bordering the inner margin of the sporogenous tissue form the inner tapetum. The tapetal cells are usually binucleate, separating later as they undergo various form changes. In the tomato, it appears to be typical that metaphases, anaphases, and telophases of the second reduction division may occur simultaneously in a single locule. No wall formation takes place until both nuclear divisions are completed. The microgametophytes are binucleate, containing a generative and tube nucleus; and, following pollination, the generative nucleus divides before the pollen tube reaches the megagametophyte.

POLLINATION.—Dehiscence of the stamens begins 24 to 48 hours after the opening of the corolla. Each locule contains several hundred pollen grains, and the anthers split longitudinally in an introrse manner so that the pollen may fall directly on the stigmatic surface of the pistil. Namakawa (25) has investigated dehiscence in several solanaceous plants including tomato; and, although there is some variation in detail, the general mechanism is relatively constant. The epidermis at the point of abscission is underlaid by a special disjunctive tissue that is from one to seven layers in thickness. Anthesis may occur in one of three ways: by the solution of the middle lamella of the epidermal cells along the line of dehiscence; by the solution of the entire wall of such epidermal cells; or by mechanical rupture of the epidermis due to hygroscopic action of a fibrous layer of cells in the anther wall.

The type of dehiscence, the pendent position of the flowers, and the fact that the stigmas are receptive to pollen one or two days before the anthers split, usually result in self-pollination. Some crossing does occur, however, and as much as a 5 per cent cross-pollination has been recorded in certain long-styled varieties in which the style and stigma project beyond the staminal cone. Where cross-pollination does occur, it is carried on through the

agency of insects, the bumblebee, according to Fink (9), being the most common visitant.

The growth of the pollen tube is relatively slow even at optimum temperatures. According to Smith and Cochran (29), these are 70° to 85° F. for the best germination and 70° for the maximum growth of the pollen tube. Under favorable conditions, no case was found by them where fertilization could be observed in less than 50 hours after pollination. Germination and growth were very poor on either side of the optimum temperatures at 50° and 100° F. respectively.

MEGASPOROGENESIS. — Many ovules are developed on the massive fleshy cauliné placentae, and they completely cover the free surfaces at about the time that the microspore mother cells undergo the first reduction division in the anthers. The ovules develop as erect globular protuberances on the placental surface; but the growth of the ovule is not uniform, and it becomes anatropous as a result of a more rapid cell division on one side of the primordium. (Fig. 293, A.) It develops a single, massive integument that completely encloses the nucellus, except for the micropylar opening, by the time the four megasporangia are formed. The cells divide in all planes so that the integument increases in thickness as well as in length. A single vascular strand is differentiated from the placental bundles which passes through the funiculus terminating in the chalazal region of the ovule.

According to Cooper (8), the hypodermal archesporial cell does not divide to form a primary parietal and primary sporogenous cell; but functions directly as the megaspore mother cell. By the time young microspores have developed in the anther sacs, the megaspore mother cell is undergoing its first or heterotypic division; and, as a result of reduction divisions, a linear row of four megasporangia is formed. Of these, the megaspore at the chalazal end forms the megagametophyte and the other three disintegrate. The growth of the megagametophyte is rapid, and three successive nuclear divisions result in the formation of an eight-nucleate gametophyte, after which the two polar nuclei fuse so that the mature megagametophyte is seven-nucleate. The two synergids and the megagamete are located at the micropylar end of the gametophyte, while the three more or less triangular antipodal cells lie at the chalazal end and have a tendency to disintegrate rather early. As the nucellar tissue is resorbed, the

inner cells of the integument elongate perpendicularly to the surface of the gametophyte, forming a nutritive layer that has been inaccurately designated as a "tapetum."

EMBRYOGENY. — Souèges (31, 32) and Tognini (34) have given detailed accounts of the embryogeny of several species of Solanaceae, and *Lycopersicum* has been investigated recently by Smith (27). Following fertilization, the zygote divides transversely to form a two-celled embryo; and transverse divisions of these two

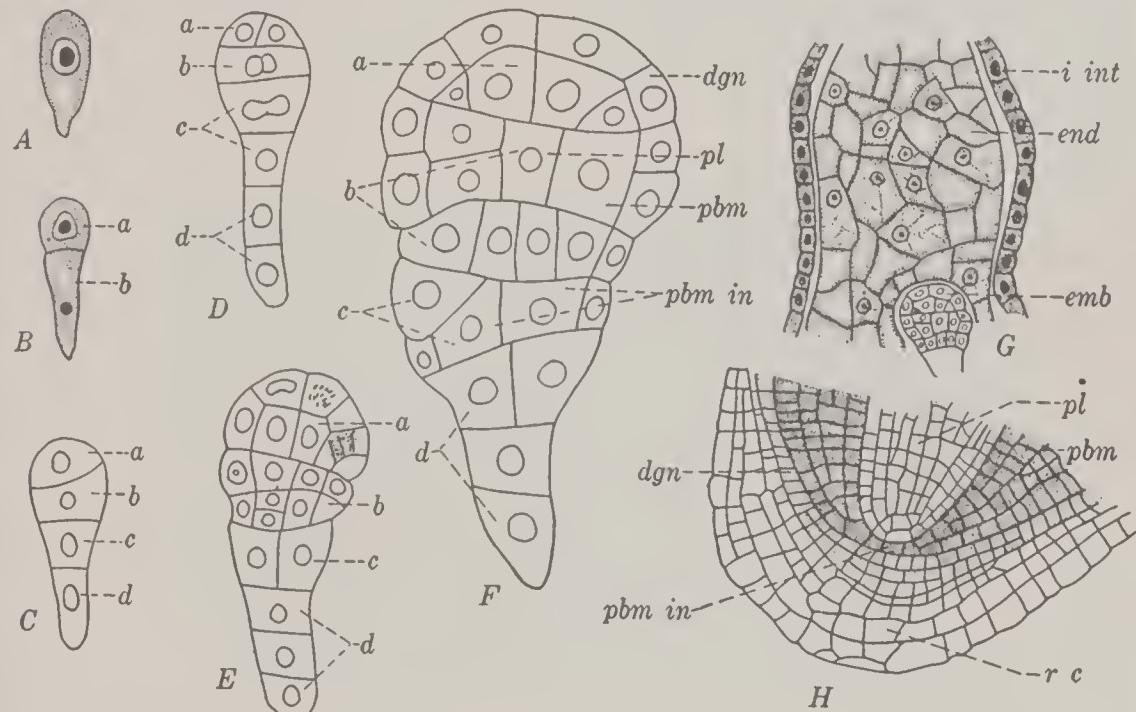


FIG. 295. *A*, fertilized egg or zygote 54 hours after pollination; *B*, two-celled embryo; *C*, four-celled embryo, 110 hours after pollination; *D*, eight-nucleate embryo, 124 hours after pollination; *E*, embryo in which dermatogen cells are cut off in tiers *a* and *b*, 130 hours after pollination; *F*, embryo with dermatogen, periblem, and plerome differentiated, 224 hours after pollination (letters *a*, *b*, *c*, and *d* refer to four tiers or regions of development in embryo, described in text); *G*, portion of longisection of ovule showing development of embryo, endosperm, and inner layer of integument, same age as *F*; *H*, longisection of basal end of embryo when fruit is about 50 mm. in diameter, showing development of histogens: *dgn*, dermatogen; *emb*, embryo; *end*, endosperm; *i int*, inner layer of integument; *pbm*, periblem; *pbm in*, periblem initials; *pl*, plerome; *r c*, root cap. (Redrawn after Smith, Cornell Agr. Exp. Sta. Mem.)

cells, *a* and *b*, result in the formation of a four-celled embryo with its cells in linear arrangement. (Fig. 295, *A*, *B*, *C*.) Smith found two-celled embryos about 44 hours after fertilization, and the four-celled stage after 110 hours. From this linear series of four cells, the ontogeny of the embryo follows a regular and uniform sequence in most of the Solanaceae. The apical cell, *a*, gives rise to the cotyledons; cell *b* produces the hypocotyl and primary root; the root cap and part of the suspensor come from cell *c*, and

the remainder of the suspensor from cell *d*. Thus, following the formation of the linear series of cells of the four-celled embryo, the cells *a*, *b*, *c*, and *d* divide to form tiers of cells from which the parts of the embryo are differentiated as noted above. (Fig. 295, *D*, *E*, *F*.) Smith observed 22-celled embryos after 130 hours, and the development of the histogens (dermatogen, periblem, and plerome) occurred after 224 hours. The formation of the cotyledons takes place in about 18 days and the primary root shows a definite histogenic organization at that time. (Fig. 295, *H*.)

The development of the endosperm precedes that of the embryo, and the division of the primary endosperm nucleus begins in advance of that of the zygote so that there may be an endosperm of 8 or more cells before the two-celled embryo is formed. Between 94 and 130 hours after pollination, there are definite walls formed in the endosperm; and at the end of 190 hours, it completely fills the embryo sac surrounding the young embryo. (Fig. 295, *G*.) In some cases, the adaxial faces of the cotyledons are closely appressed, forming a single coil (Fig. 298, *A*), while in others they are curved away from each other. (Fig. 297, *A*.)

THE FRUIT. — The fruit is a large berry which is globular or oblate in the principal commercial varieties, but may be elongated or pear-shaped in some of the special types. The very small cherry tomatoes sometimes weigh but a fraction of an ounce, while the table and market varieties weigh from $4\frac{1}{2}$ to 6 or 7 ounces, and some of the largest canning types, especially the Santa Clara, may attain a weight of 9 to 12 ounces. (Fig. 296.) As seen in transection, the fruit has from two to twenty or twenty-five locules, the smaller numbers occurring in small-fruited forms and in the wild types from which the cultivated varieties have been derived. The principal commercial varieties have five to nine locules, except for the large canning types which have the maximum number indicated.

The quality of the fruit is dependent upon color, flavor, shape; and, structurally, upon the relative amount of outer and inner wall tissue. MacGillivray and Ford (23) divided the tomato into five fractions (outer and inner wall, inner locule tissue, gelatinous pulp, skin, and seed) and computed the percentage composition of each in order to determine their relation to quality. On this basis, they concluded that "the outer and inner wall region of a tomato fruit is the most valuable in producing tomatoes of high

quality" because it contains the highest percentage of dry material, the highest percentage of insoluble solids, and possesses the sweetest taste owing to its high percentage of reducing sugar.

The time elapsing from the setting of the fruit until its maturity depends upon the variety as well as cultural and climatic conditions; but from seven to nine weeks may be regarded as an average period. Growth studies by Gustafson (12) for two varieties indicate that the growth curve for the fruit is very much like that found in the vegetative parts; that is, "there is a period of slow growth, gradually becoming more rapid until a point of maximum growth is reached, and from that time there is a slowing up." The



FIG. 296. Fruits of Santa Clara Canner variety. (Courtesy of the Ferry-Morse Seed Co.)

moisture content increases throughout the growing period, especially as the fruit passes from the green mature stage to the ripe condition; but increase in the size of the fruit occurs without an increase in the per cent of dry matter. The per cent of dry weight is highest in the immature ovary, decreases rapidly during the first two weeks of growth, and at no time is there an increase. In one variety, Gustafson found the young ovary had 17 per cent dry matter, 6.2 when two weeks old, and 5 per cent when mature, six weeks later. MacDougal (22) reported a similar situation, although the differences were not as great.

PIGMENTATION OF THE FRUIT. — The color of the mature fruit results from the presence of carotenoid pigments, lycopersicin (lycopene) and carotin (carotene). Their distribution in the tissues of the pericarp and the proportionate amounts of each

pigment determine the variation in the shade and intensity of color.

There are differences of opinion in regard to pigmentation in tomato fruits and two viewpoints are here reported. Jones and Rosa (16) state that

"In lemon-yellow fruit, carotin occurs in the pericarp, but the epidermis is colorless; in orange-colored fruit, carotin occurs both in pericarp and epidermis; in pink fruit, lycopersicin occurs in the pericarp, but the epidermis is colorless; in red fruit, lycopersicin occurs in the pericarp and carotin in the epidermis and probably in the pericarp as well. Albino, or white, fruit lacks all pigments."

Smith (28) sums up the matter as follows:

"It has long been advocated that there are yellow and transparent tomato skins which, combined with yellow or red fruit color, give rise to light yellow, dark yellow, pink, and orange-red tomatoes. These transparent skins have often been called *colorless*. This is erroneous. All skins of commercial red and pink tomato fruits are colored. The cell walls of yellow skins are yellow or golden, the color being due to an unidentified pigment. The cell walls of pink skins lack this pigment and therefore are colorless. The color of the pink skin is due to the presence of lycopene crystals, and often carotene also, as a part of the cell contents. Light intensity and quality appear to have an effect on the pigment content of the skins of tomato fruits by altering the quantity of any or all of the three pigments which constitute tomato-skin color."

In studies of fruit pigments, Howard (15) points out that Willstätter and Escher (37) have demonstrated that lycopersicin is identical in general composition and molecular weight with carotin. Her work on tomato indicates that lycopersicin is the principal pigment and that carotin is present in small amounts. The lycopersicin crystals which occur in the ripe fruits are brownish rose to carmen red and are usually in the form of needles or elongated prisms. In some instances, crystal aggregates are formed, while in others the crystals appear as long fine hair-like structures.

On the basis of Smith's investigations it appears that protection of the fruit from intense light favors lycopene formation; but that

"the carotenoid content of both the skin and the flesh of fruits ripened in the light is higher than in fruits ripened in the dark when the early growth has occurred under the same light conditions. To attain maximum carotenoid content, the fruits should be grown in complete exposure to light and allowed to mature on the vine."

There appears to be no direct relation between chlorophyll formation or decomposition and the lycopene content of the fruit, as Smith was able to obtain lycopene from mature fruit which had been grown in complete darkness. Furthermore, he found no evidence of lycopene in plastids or of crystals formed from plastids as a result of plastid decomposition; and he was able to demonstrate that there are numerous lycopene crystals in the epidermal cells which are plastid free. Carotene was found in granular form inside plastids as well as after their decomposition, and it also occurs in crystalline and globular forms.

STRUCTURE AND DEVELOPMENT OF FRUIT.—Structurally, the fruit consists of the pericarp, placental tissue, and the seeds. The skin of the pericarp has been studied by Groth (11). In all types, it consists of an epidermal layer within which are three, occasionally four, well-defined layers of collenchymatous tissue. The epidermis is covered by a relatively thin cuticle; and the polyhedral cells never have sinuous outlines as do those of the leaf epidermis. The number of epidermal cells does not increase greatly with growth of the fruit; and, in consequence, the epidermal cells in mature fruit are much larger than those found in young ones. Except in currant tomatoes, the epidermis develops hairs and glands that are shed as the fruit matures. The hairs are unbranched and consist of three to five cells, while the glands have a unicellular basal stalk and a top of two to four cells. Rosenbaum and Sando (26) observed that the cuticular layer increased in thickness as the fruit aged, and also noted a complete absence of stomata in the epidermis of both young and old fruits.

The major portion of the pericarp is composed of large thin-walled cells with numerous intercellular spaces; and, at the time of differentiation of the megasporangium mother cell, it is about 8 cells in thickness. According to Smith and Cochran (29), it continues to thicken, being 14 layers in thickness 60 hours after pollination, and 20 layers thick 34 hours later. Two weeks after pollination, when the fruit is about 12 mm. in diameter, the pericarp is 28 to 30 cells thick. The cells enlarge enormously during development, and this is more significant in the growth of the fruit than the increase in number of cells. As the fruit matures, some of the cells of the inner and central portion of the carpels may partially disintegrate.

As the ovules develop, there is an outward growth of the paren-

chymatous cells of the placenta which surround their bases. This can be observed within 60 hours after pollination, and the parenchyma increases until it completely encloses the developing seeds in a homogeneous tissue of thin-walled cells. (Fig. 293, C.) The cells do not unite with the carpillary walls, but press against them and the surfaces of the seeds. At first the tissue is firm and compact; but, as the fruit matures, the walls become thinner and the cells partially collapse. Large numbers of round starch grains are included in the gelatinous contents.

PARTHENOCARPY. — Parthenocarpy is not uncommon, but the fruits produced are usually small or of poor quality. Hawthorn (14) has reported a case of seedlessness in Texas in a cross between a Large Cherry variety and Bonnie Best. In this instance, the fruits contained seeds in June and usually in July; but were seedless in midsummer, and again bore seed-containing fruits in November. During the seedless period, the plants bore as profusely as at other times and produced fruits of fine quality.

It is also possible to produce seedless tomatoes experimentally by treating unpollinated flowers with various organic acids. Gustafson (13) applied organic acids in lanolin to the cut surfaces of the styles of flowers from which the stamens had been removed. Varying results were obtained with different acids, but mature fruits with perfectly normal external appearance were developed in several cases. In the larger fruits, there were occasionally well-developed locules, but the smaller ones did not form them, and in no instance were seeds produced. In general, the pericarp was thinner and the fruits more fleshy, but the water content was approximately the same as in those produced following pollination.

THE SEED. — The mature seeds are oval in outline and very much flattened laterally. (Fig. 297, A.) They vary considerably in size; and in a random sample of commercial seed averaged 3 to 5 mm. in length and 2 to 4 mm. in breadth. The surface of the buff to straw-colored seed coat is covered with gray or silver hairs and scales which are the remains of the lateral walls of the outermost cell layer of the integument.

Souèges (30) has described the development of the integument in the tomato and other solanaceous plants, including the manner in which the hairs develop. He divides the massive integument into four regions: an outer or epidermal layer which ultimately produces the hairs, an intermediate parenchymatous region which

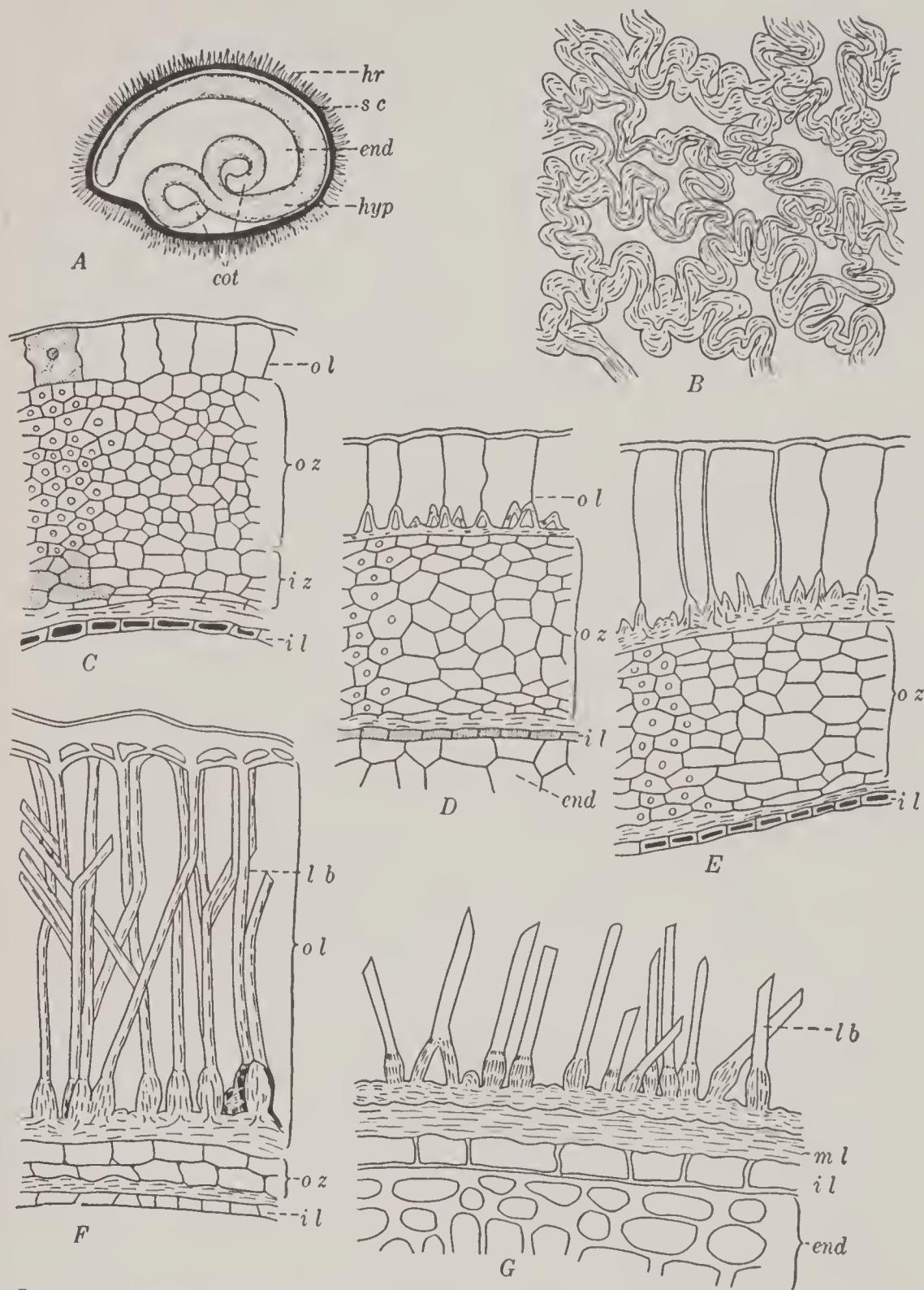


FIG. 297. A, longisection through mature seed showing position of embryo; B, transsection of outer layer of mature seed coat showing sinuous walls and character of thickening; C-G, successive stages in development of seed coat showing resorption of outer and inner zones, and development of wall thickenings of outer layer which form hairs: cot, cotyledons; end, endosperm; br, hairs or longitudinal bands produced from outer layer of seed coat; hyp, hypocotyl; il, inner layer of seed coat; iz, inner zone of parenchyma; lb, thickened longitudinal bands of wall; ml, membranous layer of mature seed coat; ol, outer layer of seed coat; oz, outer zone of parenchyma; sc, seed coat. (B-G redrawn after Souèges, Ann. Sci. Nat.)

is subdivided into an outer and inner zone, and the innermost layer or epidermis which is highly pigmented, giving color to the mature seed. (Fig. 297, C.) As the seed enlarges, the number of parenchymatous cells of the outer zone is increased by many cell divisions.

The walls of the outer epidermis develop thickenings which are initiated on the inner walls and at the base of the lateral walls. (Fig. 297, D.) While still in the fruit, the epidermal cells of the partially mature seed show longitudinal bands or thickenings that are more or less localized at the angles of the cells; and these continue to the external wall, forming a large irregular network or mesh. (Fig. 297, E, F.) During the final stages of maturation, the portions of the lateral wall between the longitudinal bands are split, and the external wall also disappears. In this manner the bands are isolated from one another and form long "hairs" or scales that cover the outer surface of the seed at maturity. (Fig. 297, G.) The basal portions of the bands are sinuous and irregular, being thickest at the angles from which the "hairs" arise. (Fig. 297, B.)

While this development is taking place, there is a gradual resorption of the intermediate zones. This is initiated in the inner zone of parenchyma and continues progressively until maturity. Nothing is left of the intermediate parenchyma except a crushed membranous layer which with the inner layer gives color to the seed. (Fig. 297, C-G.) The haustorial or digestive cells of the innermost layer are rectangular in transection and polygonal as seen in surface view.

DEVELOPMENT OF THE SEEDLING. — Although variation in the size of the seed may not proportionately affect the yield of fruit, the percentage of germination is much lower in lots of light seed as compared with lots of larger, heavier seed. Under greenhouse conditions, the seeds germinate rather rapidly; and, by the seventh day, produce a slender tap root an inch or more in length with numerous root hairs. The hypocotyledonary arch emerges from the soil, and this is followed by liberation from the seed coat of the slender linear or lanceolate cotyledons which function as the first photosynthetic leaves. (Fig. 298, B-F.)

THE PRIMARY ROOT. — The primary root resembles other solanaceous forms (potato, tobacco, eggplant) in all essential details. It has a diarch protostele and the two groups of primary

phloem lie on the flanks of the primary xylem strand, which consists usually of six or eight xylem elements. The primary phloem cells are very small, consisting chiefly of elongated parenchymatous elements. The pericycle is uniserial and the protoxylem cells abut it. The narrow cortex is three or four layers in width, the innermost one forming an endodermis with prominent Casparyan thickenings.

VASCULAR TRANSITION. — King (18) and Thiel (33) find that the vascular transition agrees in all respects with that of the

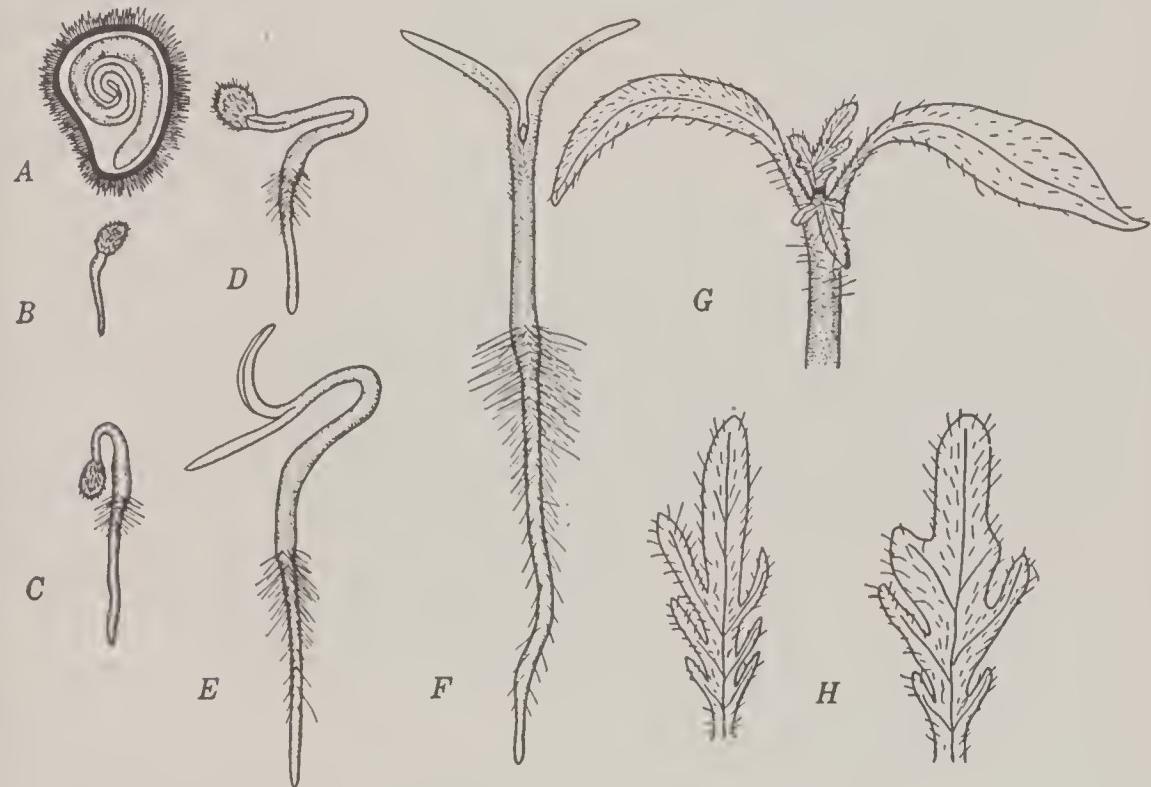


FIG. 298. *A*, longisection through mature seed showing portion of embryo and seed coat; *B-F*, successive stages in development of seedling; *G*, cotyledons and epicotyl, showing first epicotyledonary leaves; *H*, types of first foliage leaves.

potato and eggplant. The first stage in the reorientation from the exarch, radial protostele of the root to the bicollateral endarch arrangement is the separation of the diarch xylem strand into two units by parenchymatous cells. At the same time, each group of primary phloem divides into three smaller strands; and, at higher levels, the central one of each group is differentiated progressively toward the center, forming the inner phloem of the hypocotyl.

The xylem units bifurcate, and the two metaxylem portions of each divided bundle differentiate along two oppositely directed curves. (Fig. 299.) Above this point, the metaxylem is dif-

differentiated tangentially, approaching the periphery of the stele more closely; and the protoxylem develops in a more centrad position. The relation of the proto- and metaxylem is not completely endarch at the level of the cotyledonary plate. Coincident

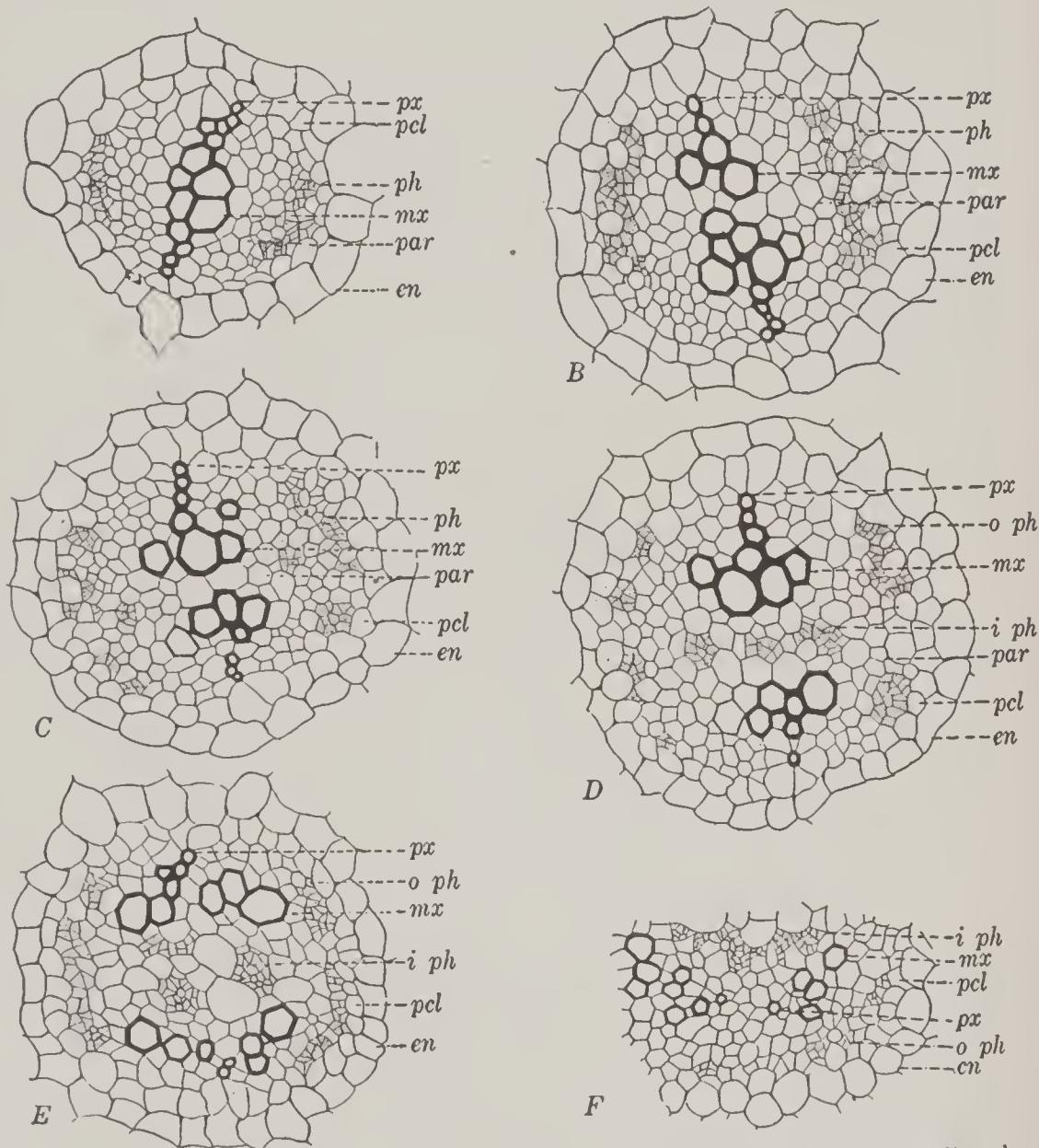


FIG. 299. A-F, successive stages in vascular transition from diarch, root-like, lower hypocotyl to cotyledonary node. Completely endarch bicollateral bundles occur in cotyledonary petiole: *en*, endodermis; *i ph*, inner phloem; *mx*, metaxylem; *o ph*, outer phloem; *par*, parenchyma; *pcl*, pericycle; *ph*, phloem; *px*, protoxylem. (After King.)

with the reorientation of the xylem, the strands of inner phloem form two groups that are located on the inner faces of the primary xylem groups, and the outer phloem is oriented outside them. As a result of adaxial differentiation of the protoxylem and abaxial orientation of the metaxylem in the cotyledon, the endarch condi-

tion is definitely attained and a bicollateral cotyledonary bundle is formed. (Fig. 299.) The traces of the first foliage leaves above the cotyledonary plate consist of bicollateral bundles that are completely endarch. These anastomose with the vascular elements of the hypocotyl at and slightly below the cotyledonary node.

SECONDARY ROOTS. — The lateral and adventitious roots are commonly tetrarch, occasionally pentarch. (Fig. 300.) Second-

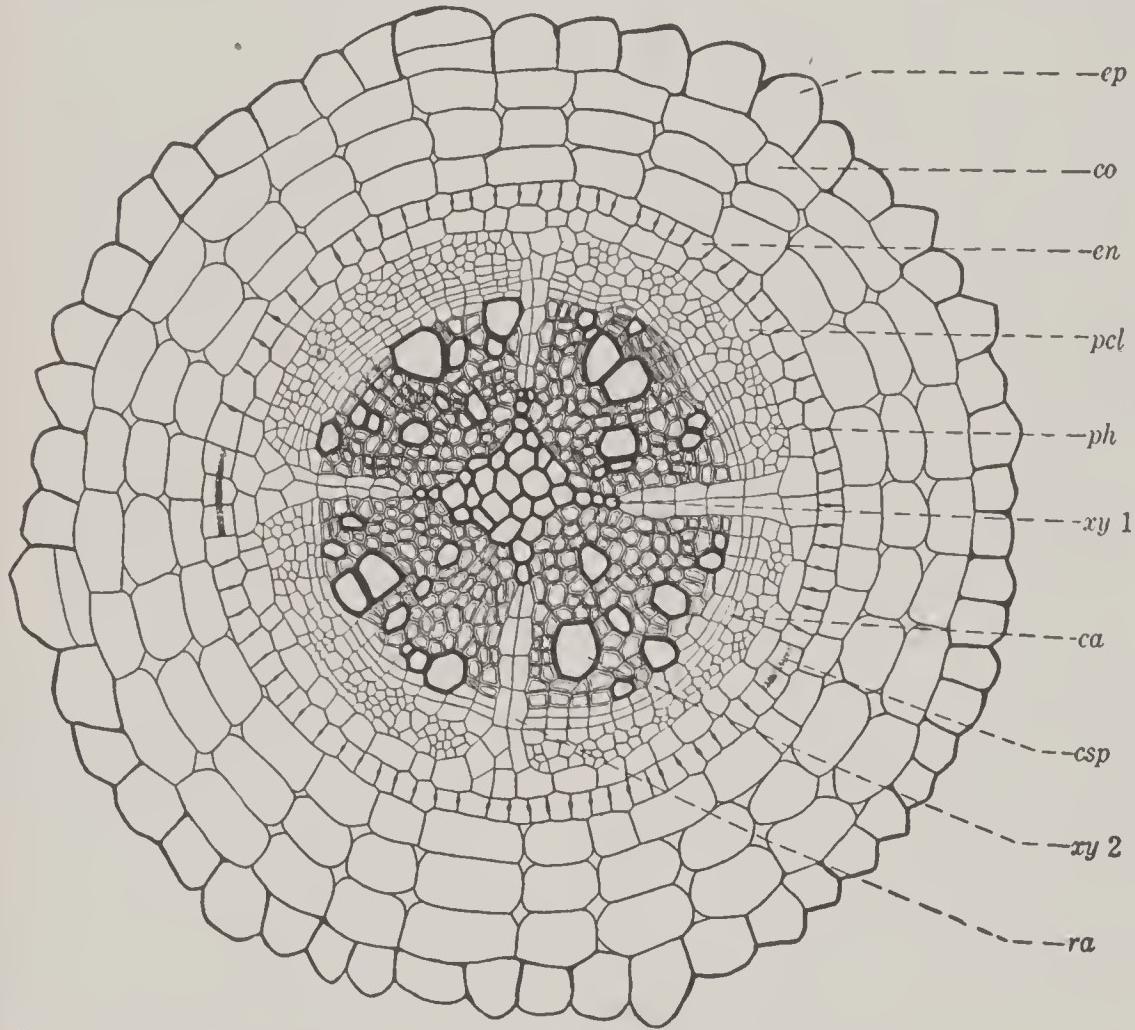


FIG. 300. Transection of adventitious root with tetrarch stele: *ca*, cambium; *co*, cortex; *csp*, Caspary strip; *en*, endodermis; *ep*, epidermis; *pcl*, pericycle; *ph*, phloem; *ra*, ray; *xy 1*, primary xylem; *xy 2*, secondary xylem.

ary thickening is initiated in the usual manner in the fundamental parenchyma centrad to the primary phloem and between the radiating arms of protoxylem. As a result of cambial activity, four wedge-shaped sectors of secondary xylem are formed which are separated from one another by pericyclic rays. Except in the ray region, the pericycle is uniseriate or occasionally two-layered. The endodermis and cortex persist for some time after secondary

thickening has begun owing to tangential enlargement and radial cell division. Lateral roots arise from sectors of pericyclic cells on each side of the protoxylem points so that they come out at oblique angles to the xylem strand between the protoxylem point and the adjacent primary phloem. For this reason, the number of rows of lateral roots is double the number of protoxylem points.

Adventitious roots originate in the parenchyma of the phloem and pericycle of the stem. The root primordium is usually located on the same radius as a medullary ray, and centripetal differentiation of vascular tissue involves ray parenchyma and some phloem parenchyma laterally. As the growing point of the adventitious root increases in diameter, its lateral extension forces the pericyclic fibers apart; and there is a displacement of the cortical cells in addition to a resorption of tissue as the root penetrates the cortex and epidermis. The rupture of the epidermis results in the formation of wound tissue, and a phellogen produces cork cells adjacent to the basal portion of the adventitious root.

THE STEM. — The stem has a dissected amphiphloic siphonostele in which the bicollateral bundles are at first separated by broad medullary rays. Later in ontogeny, the fascicular and interfascicular cambium form a continuous cylinder, and a solid zone of secondary xylem is produced. The inner phloem is not restricted to points directly centrad to the primary xylem of the bicollateral bundles, but forms a ring of scattered phloem strands that are separated from each other and from the xylem by parenchymatous cells. The outer phloem strands also form a discontinuous ring at first, but this zone becomes more or less continuous as a result of the development of secondary phloem. The secondary xylem formed by the fascicular cambium consists of large vessels and wood parenchyma, while the interfascicular cambium produces chiefly connective or conjunctive tissue. Centrad to the inner phloem are groups of inner pericyclic fibers that are less numerous than those of the outer pericyclic region and parenchymatous cells separate the fiber groups. The endodermis can be recognized by the presence of starch, and Casparyan strips may develop under certain conditions.

Immediately inside the epidermis is a zone of chlorenchyma and centrad to it there is a band of collenchyma. The collenchymatous region is more strongly developed and the cells are thicker angled in the more vegetative axes. Anderson (1) has

made microchemical and physical tests of the stem at different developmental stages, and finds that the thickened angles of the walls of the collenchymatous cells are composed of a large number of fine cellulose lamellae which alternate with layers of a pectic compound. The epidermal cells may develop to form either of the two types of hairs noted for the flower and leaf. The stomatal frequency is about half that found in the upper epidermis of the leaf.

The character and amount of secondary xylem formed is variable, depending upon the degree of vegetativeness of the stem. As Kraus and Kraybill (19) have pointed out, highly vegetative plants grown with an abundant supply of available nitrogen have stems that are much larger than those of feebly vegetative ones, owing to the greater number and size of the pith cells. There is a reduction in the amount of collenchyma and pith, accompanied by a marked increase in the secondary xylem and a conspicuous increase in the thickness of the walls of the pericyclic fibers in the feebly vegetative stem. (Fig. 301.)

THE LEAF. — The blade of the leaflet is thin, the mesophyll consisting of a single row of palisade cells and a very loosely organized spongy region of four or five layers of chlorenchyma. The major portion of the vein projects prominently on the lower surface, and there is a band of abaxial collenchyma reinforcing it which with the adaxial strand and the mechanical elements of the bundle gives support to the leaflet. (Fig. 302, A.) The b collateral bundle is like that of the stem, and there may be some cambial activity in the larger veins. In the smaller veins, the xylem consists chiefly of spiral elements. Both adaxial and abaxial phloem are present in the main laterals, but adaxial phloem is not found in the smaller branches. The walls of the cells of the upper epidermis are much less sinuous than those of the lower surface, and the stomata and hairs are less abundant on the latter. (Fig. 302, C, D.) The two types of hairs are similar to those described for the floral parts and the stem.

In the petiole, the epidermis is pubescent, and underlying it is a continuous zone of chlorenchyma three or four cells in width. Centrad to the chlorenchyma there is an uninterrupted band of collenchyma which is three to six cells in width, and within this is the parenchymatous tissue that surrounds the vascular strands. The vascular strands are arranged in an approximate circle that is

open toward the adaxial surface, and the individual bundles are separated from each other by parenchymatous rays of varying

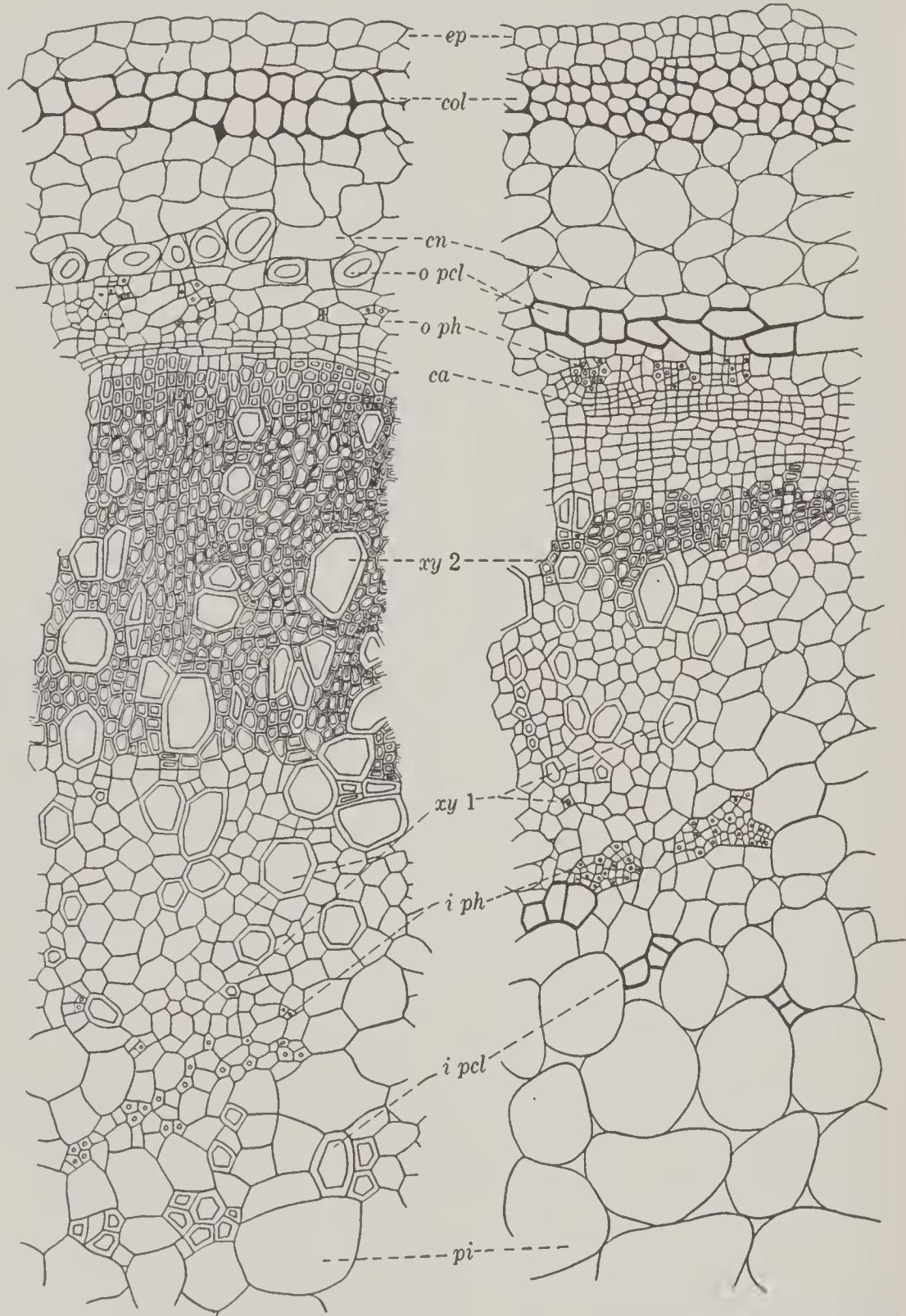


FIG. 301. Transections of sectors of stems showing: left, feebly vegetative stem; and right, highly vegetative one: *ca*, cambium; *col*, collenchyma; *en*, endodermis; *ep*, epidermis; *i pcl*, inner pericycle; *i ph*, inner phloem; *o pcl*, outer pericycle; *o ph*, outer phloem; *pi*, pith; *xy 1*, primary xylem; *xy 2*, secondary xylem. (Redrawn from Kraus and Kraybill, *Ore. Agr. Exp. Sta.*)

widths. In older petioles, some of the bundles may become interconnected by the development of an interfascicular cambium.

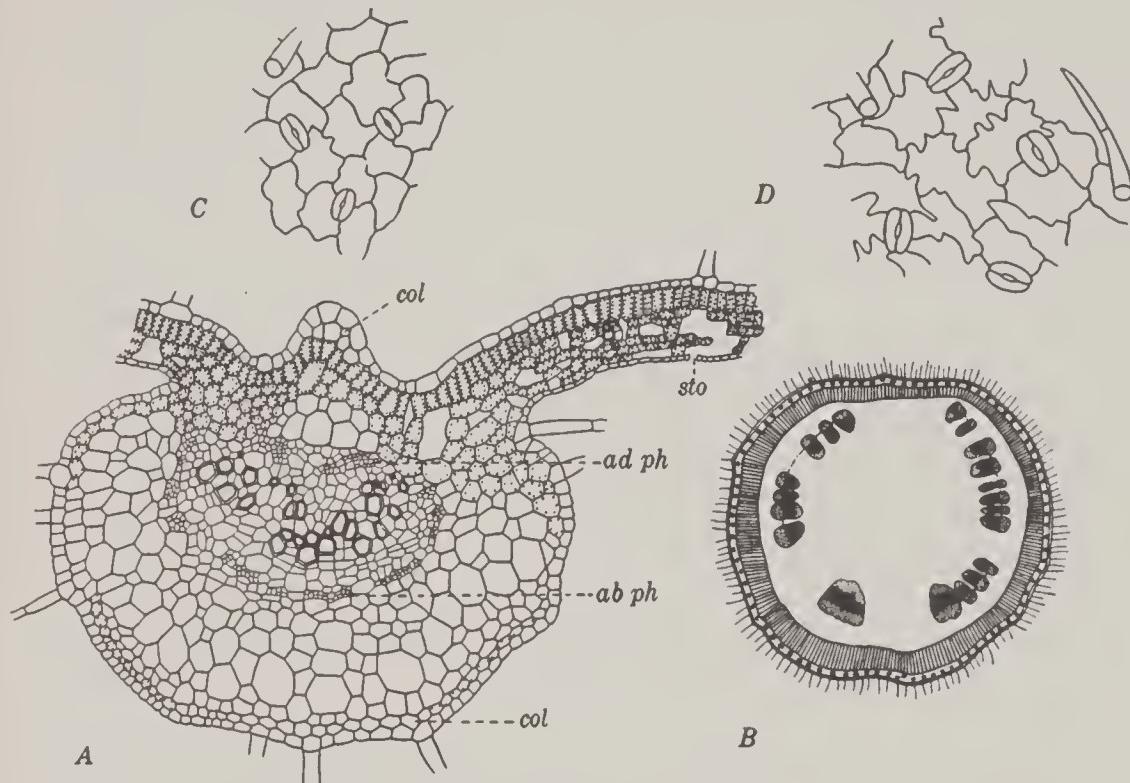


FIG. 302. *A*, transection of portion of leaflet including midvein; *B*, diagrammatic transection of petiole of leaf; *C*, portion of upper epidermis showing distribution of stomata; *D*, same of lower epidermis. In *B*, zone of mechanical tissue inside chlorenchyma is lined, outer and inner phloem are stippled, xylem is black, and developing interfascicular cambium is indicated by dots: *ab ph*, abaxial phloem; *ad ph*, adaxial phloem; *col*, collenchyma; *sto*, stoma.

(Fig. 302, *B*.) The individual b collateral bundles are similar in organization to those of the stem.

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CHAPTER XIX

CUCURBITACEAE

CUCURBITA spp.

THE gourd family, Cucurbitaceae, is widely distributed and includes approximately 90 genera, most of which are tropical or subtropical, although a few forms occur in the native flora of the colder portions of the temperate zone. Three genera are cultivated for their edible fruits: *Citrullus*, the watermelon; *Cucumis*, the cucumber and melons; and *Cucurbita*, which includes pumpkins, squashes, and gourds. In the genus *Cucurbita* three species are extensively grown, *C. Pepo* L., *C. maxima* Duchesne, and *C. moschata* Duchesne, commercial varieties of the first two being the most generally used. Under cultivation the three species grow as annuals; and, although sensitive to frost, they develop with such rapidity that some varieties are grown in the northern states.

GENERAL MORPHOLOGY

THE Root. — The root system is characterized by a strong tap root which, according to Weaver and Bruner (39), may penetrate to a depth of 6 feet at maturity although branching is not extensive below the two-foot level. The branches spread widely, occupying a radius of nearly 20 feet, and the main laterals have numerous secondary branches 2 to 8 feet long which in turn branch until there is a remarkable network of rootlets that completely occupies the soil near the surface. In addition to the primary root system, the adventitious or nodal roots may attain a length of 4 to 5 feet, and they also branch so that the absorbing area is much increased.

THE SHOOT. — In general, the plants have prostrate vine-like stems, but some varieties of *C. Pepo* are more or less bushy and semi-erect. In the latter, the internodes are much shortened, as compared with the trailing types, and tendrils are absent. In the prostrate forms, three to several lateral branches arise from nodes near the base of the stem axis; and extend outward for

many feet, having a tendency to produce adventitious roots at the nodes. The growth of these branches is extremely vigorous, and Holroyd (18) has stated that "members of this group may form a growth of stem and leafage within the growing period of four months that is probably unequaled by any other annual herbaceous plant family." In *C. Pepo*, he has reported an instance in which a single plant developed stem and branch growth exceeding 140 feet in total length, from which were diverged as many as 450 leaves.

The stems are roughly five-angled, hollow at maturity, and bear multicellular hairs or trichomes which are either sharp-pointed and conical or long-stalked, capitate, and glandular. The branching is of the sympodial type in which a lateral branch continues the stem axis; and, by its growth, displaces the terminal branch so that the latter occupies a position on the opposite side of the axis from the leaf which arises at that node. The terminal branches form the tendrils which may be simple or have three or four branches. (Fig. 303.) The tendril is generally interpreted as a shoot, the basal portion being the branch, and the terminal portion a specialized leaf.

The large cordate leaves are petiolate and usually three- to five-lobed, the prominence of the lobing varying with the species and variety. In *C. Pepo*, the hairy leaves are commonly five-lobed, sometimes three, and frequently have white spots at the angles of the veins. In *C. maxima*, the leaves are usually without lobes or with short, rounded ones; and in *C. moschata*, they are lobed but more nearly orbicular in outline than in *C. Pepo*. The texture of the leaves is variable, being somewhat harsh in *C. Pepo* and less so in the other two species.

THE INFLORESCENCE. — The yellow flowers are monoecious and occur singly in the axils of the leaves. In trailing varieties, the



FIG. 303. *Cucurbita Pepo* showing sympodial branching and relative position of tendrils and inflorescences, variety Table Queen.

staminate flowers are located near the center of the vine and are borne on slender peduncles; while the pistillate flowers are borne on short ridged stalks, distal to the staminate ones. In the bushy types, the pistillate flowers occur near the base of the plant. The character of the peduncle is sufficiently distinct in the three species to be used as a diagnostic character. In *C. Pepo*, the fruit stalk is deeply furrowed and five- to eight-ridged; in *C. moschata*, it is five-ridged and enlarged next to the fruit, and in *C. maxima*, the peduncle is cylindrical or claviform but never prominently ridged.

THE CARPELLATE FLOWER. — The carpellate flowers are epigynous. The calyx tube is terminated by five slender awl-shaped lobes, and the campanulate corolla is also deeply five-lobed; the lobes being recurved at the tips. (Fig. 304, A, B.) The pistil consists of three carpels which form a three-loculed ovary, and the thick, short style is terminated by three bilobed or divided papillate stigmas. Occasionally, the pistil may consist of four or five carpels with a resultant four- or five-celled ovary. The stamens are rudimentary, three staminodia being commonly present; and a ring-like nectary is located between the base of the perianth tube and the style. (Fig. 305, A.)

The development of the pistillate flower has been investigated by Kirkwood (22) for several genera of Cucurbitaceae; and by Judson (21) for *Cucumis*, as well as by several of the earlier morphologists, including Payer (31) and Goebel (13). These accounts are in general agreement, except for differences in the interpretation of the development of the ovary and the character of its placentation.

The floral axis first develops as a rounded protuberance which elongates. The apex then becomes flattened, and a slight terminal depression develops so that the surface is somewhat concave. The primordia of the floral parts arise from this surface in acropetal succession: sepals, petals, staminodia, and carpels. Because of differential growth at five points on the margin, outgrowths arise which are the primordia of the sepal lobes. Growth of these lobes, and of the underlying tissue at the outer margin of the receptacle, results in an elevation of the outer border of the receptacle; and the inward curvature of the densely pubescent lobes tends to cover the tip of the floral axis. At this time, the central portion of the stem apex grows slowly; and the more rapid growth of the outer portion forms a cup-shaped receptacle which surrounds it.

The primordia of the petals appear shortly after those of the sepals and alternate with them. They form a cycle of five small, blunt protuberances which at first grow less rapidly than the sepal primordia; but later accelerate their growth and, like the sepal lobes, form an enclosing protective envelope over the tip of the receptacle. These primordia are also pubescent but the hairs are less rigid than those on the sepals. The development of these two cycles of primordia, which ultimately become the lobes of the calyx and corolla respectively, is accompanied by the growth of the undiverged tissues immediately below them, which results in the formation of a continuous cylinder of tissue constituting the perianth tube.

One of the three rudimentary stamens is smaller than the other two, each of which arises opposite a petal lobe. The small one is located in an interval between a petal lobe and a sepal lobe and the spacing is such that the three are equidistant from one another within the perianth tube. They appear shortly after, or in some cases coincident with, the origin of the petal primordia; the smallest staminodium appearing first, and the second and third arising in a counter-clockwise direction. At first, the staminodia are conspicuous; but, as the flower develops, their growth is arrested and their terminal portions may become withered and dried. The continued growth of the perianth tube, below the point of divergence of the staminodia, gives them the appearance of diverging from a midpoint in the perianth tube.

Following the appearance of the staminodia, three small lobes arise equidistant from one another at the bottom of the cavity of

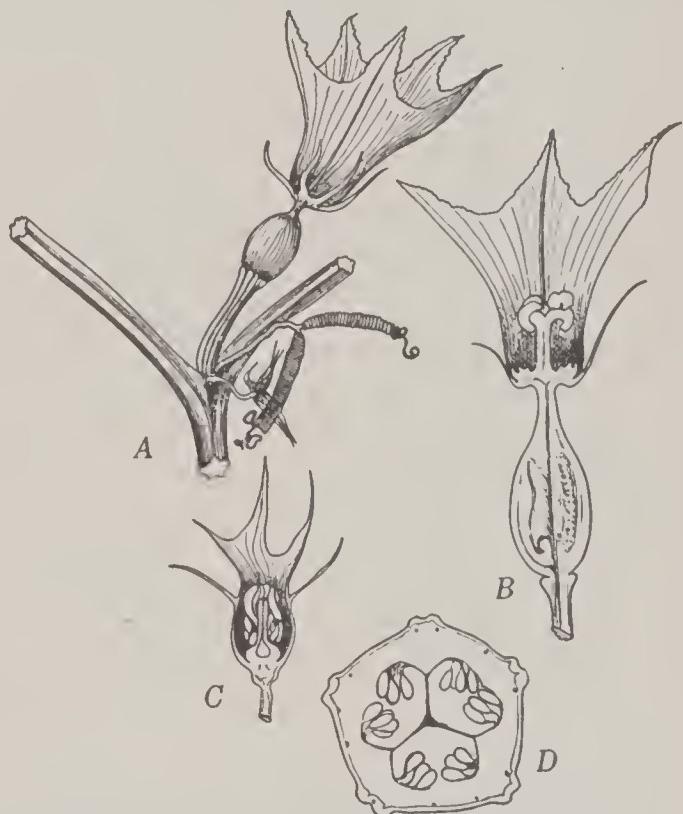


FIG. 304. *A*, habit of pistillate flower; *B*, median longisection showing epigynous character; *C*, longisection of staminate flower with abortive pistil; *D*, transection of tricarpellate ovary showing placentation.

the receptacle, below and centrad to them. These carpillary primordia grow in such a way that they form three crescentic structures with edges extending toward the center of the ovary, and with abaxial surfaces that are adnate to the receptacle except at their distal ends. The growth of their inturned edges results in the formation of three ridges, each of which represents the edges of two adjacent carpillary margins. As centripetal growth of the ridges proceeds, they reach the center of the ovary and

ultimately fill it except for three narrow spaces which form a triradiate cavity. (Fig. 305, B.) When the infolded edges of the carpels reach the center of the ovary, they curve outward, grow centrifugally until they approach the outer wall of the locule, and then again turn inward toward the center of the ovary. The infolded edges of each carpel form the placentae from which the ovules arise; and in *Cucurbita*, *Citrullus*, and to a lesser degree in *Cucumis*, each placenta becomes a multiple structure with two or three longitudinal ridges on each placental

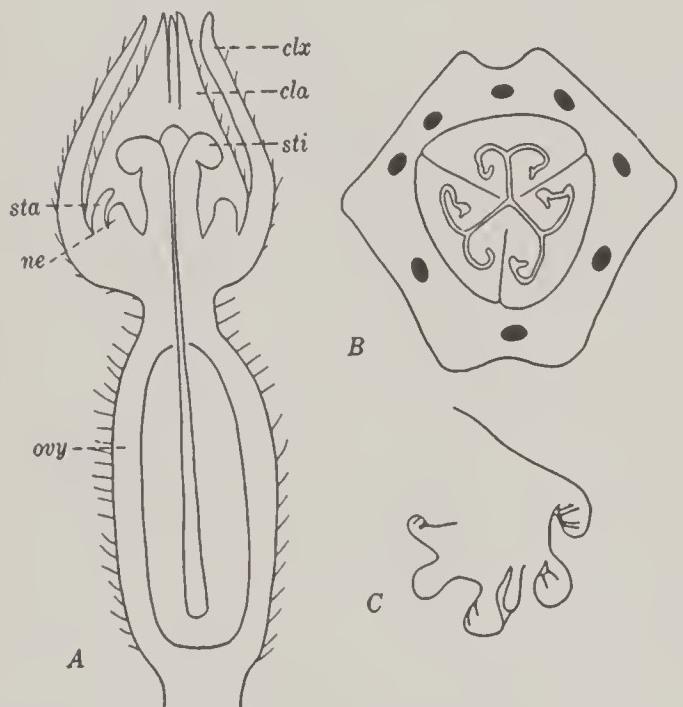


FIG. 305. A, diagrammatic longisection of young carpellate flower showing epigyny; B, transection of ovary with three locules and multiple placentae; C, diagram illustrating placenta, origin of ovules and their comparative development: *cla*, corolla; *clx*, calyx; *ne*, nectary; *ovy*, ovary; *sta*, staminodia; *sti*, stigma. (C redrawn from Kirkwood, *Bull. New York Bot. Gard.*)

margin. (Fig. 305, B, C.) In this manner, each carpel develops a series of ovules of varying ages borne on parallel placental ridges. Owing to the position in which the placental ridges are finally oriented, the placentation has been described as parietal by some investigators; but it is probably better to regard it as axile or central placentation, plus a centrifugal overgrowth which carries the placentae toward the periphery of each locule.

The most fully developed ovules are located on the placental ridge farthest from the margin of the carpel, while the smallest ovules are found on the placental fold nearest the margin. As the

flower reaches anthesis, however, the difference in the relative development of the ovules is somewhat equalized so that the chances for fertilization are about the same for all. The ovules appear first as small papillae on the margins of the placentae and become strictly anatropous at maturity.

The growth of the upper portions of the carpels results in the formation of three undiverged styles, and the three stigmas are distinct, appearing as bilobed or divided structures. The tissue of the ring-like nectary is derived from the receptacle at the base of the perianth tube, after the carpillary lobes have grown upward to form the styles and stigmas. (Fig. 305, A.)

THE STAMINATE FLOWER. — The number of staminate flowers produced always exceeds that of the pistillate ones. They have a campanulate corolla, which with the calyx forms an undiverged basal perianth tube. The lobes of the latter are linear and alternate with the five deeply lobed segments of the corolla. (Fig. 304, C.) The three stamens are not alike, as two of them are tetrasporangiate, producing two locules at maturity, while the third is bisporangiate and unilocular. The filaments are free, but the stamens are more or less united by their anthers, which grow vigorously in length, forming long vermiform coils. (Fig. 306.)

The sequence of development of the floral parts, according to Heimlich (16), is perianth tube, stamens, pistillodium, calyx lobes, and corolla lobes. As in the carpellate flower, the floral axis is at first club-shaped, but its apex soon broadens and the ring-like fold of the perianth tube is formed. This is followed by the differentiation of the primordia of the stamens, which arise in a close spiral arrangement, the first one to develop being a unilocular stamen which is sometimes referred to as the "half stamen." The second stamen develops in a position opposite the leaf in the axil of which the flower arises, and the third is formed at a point that is equidistant from the other two. The three primordia of the pistillodium then develop in a close spiral, their lobes alternating with the stamens.

Each stamen develops a wide filament with a broad connective which supports the anther. The filaments are diverged from the receptacle at the base of the inner surface of the perianth tube; and, within the staminal cycle, a slightly-lobed, ring-like nectary is developed which encircles the pistillodium. The rudimentary

carpels may attain varying degrees of development, occasionally forming a mature pistil so that a perfect flower results.

As the stamens are developing, the calyx and corolla lobes arise from the margin of the perianth tube in a spiral arrangement and the broad thin corolla lobes overarch the androecium. Large intercellular spaces develop in the parenchymatous tissue of the perianth tube, and these schizo-lysigenous cavities finally extend from near its base to the point of divergence of the corolla.

The morphological interpretation of the dissimilar stamens which constitute the androecium of some of the cucurbits has been a controversial matter. Heimlich (16) has supported the

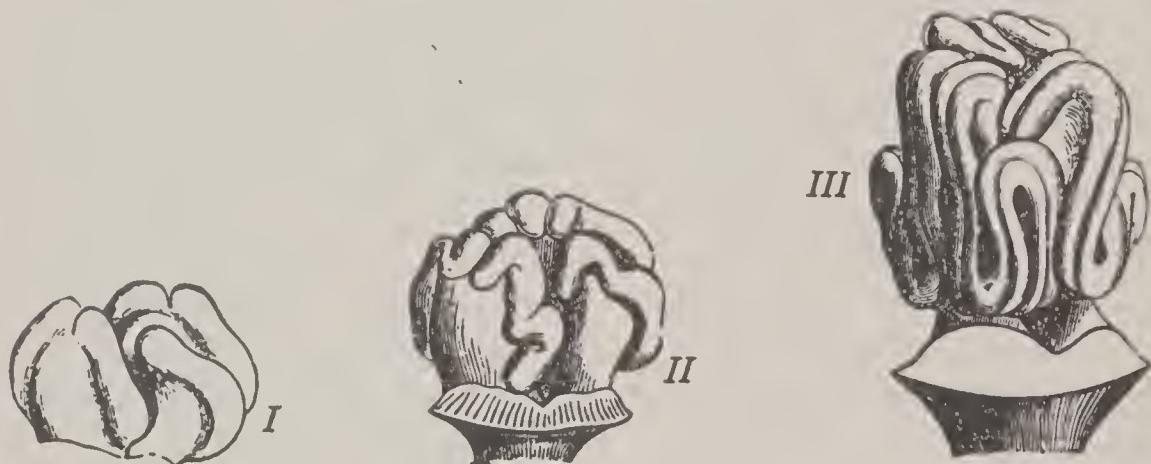


FIG. 306. Development of androecium; the single stamen is to right in each figure, while behind and to left are two double ones. (From Sachs, after Payer, *Textbook of Botany*, Clarendon Press.)

original interpretation of Naudin (30) that the two bilocular stamens are complete; and that, in the third, one locule fails to develop. Miller (28), comparing *Echinocystis* with other genera, has concluded that the bisporangiate, unilocular stamen is a complete one and not a "half organ" in the developmental sense. On this basis, he regards *Cucumis* and *Cucurbita* as having "five stamens, four of which are united in two masses," and agrees with Eichler (8) and van Tieghem (36), who regarded the tetrasporangiate, bilocular stamen as a double organ. Miller based his interpretation upon the observation that the tetrasporangiate stamen in *Echinocystis* arises from two separate primordia which form a single structure owing to lateral coalescence and the growth of intervening tissue between the original primordia.

A peculiarity of the pollen tube has been observed in the cucurbits by Longo (27), and Kirkwood (23) has confirmed this point. Longo found that the pollen tube expands into a large bulla at

the base of the neck of the nucellus. It then develops branches which traverse the nucellus and the inner integument, also maintaining an intimate connection with the internal layers of the outer integument. This behavior of the pollen tube has a functional significance, according to Longo, since the branches of the tube act as haustoria in the translocation of nutritive material.

THE FRUIT. — The fruit of the cucurbits is one of the largest found in the plant kingdom. It is indehiscent with the fleshy receptacle adnate to the pericarp, and is classified as an inferior berry or pepo. The varieties of squash and pumpkin are numerous,

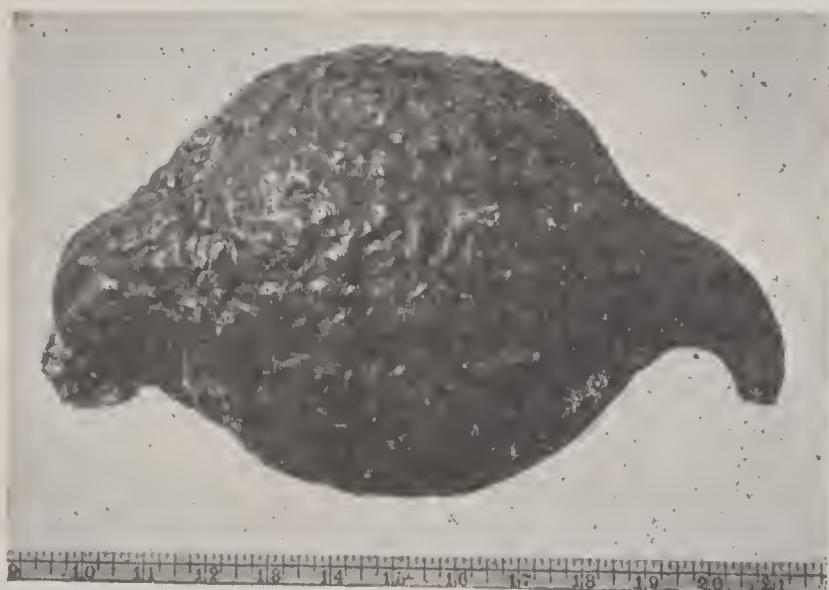


FIG. 307. The fruit of Hubbard Squash. (Courtesy Bur. Plant Industry.)

and the list is constantly increasing owing to hybridization and experimental breeding, so that there are wide variations in fruit characters, especially with respect to shape, size, texture of the skin, and color. Varieties of *C. Pepo* have fruits some of which are round, flat, and scalloped at the edges, or elongated and crooked-necked; while others are short and club-shaped, or acorn-shaped and variously grooved. Varieties of *C. maxima* include the Hubbard squash which is roughly elliptical, tapering to a curved stem end, and others that are turban-shaped owing to the fact that the fleshy receptacle and the ovary are diverged for a longer distance than is usually the case. (Fig. 307.) Those of the banana type are elongated and somewhat pointed at the ends. In *C. moschata* the fruits are also variable in shape, some having long curved necks while others are more oval or spherical. The surface may be smooth, warty, or covered with spines and other types of

emergences. The young fruits of practically all varieties bear hairs of one or more kinds which may or may not persist until maturity. The skin may be white, green, yellow, red or, in some cases, variously spotted and striped.

ANATOMY

ANATOMY OF THE FRUIT. — Despite the pronounced variation in shape, size, and color, the anatomical characters are fairly constant; and Barber (2) has pointed out that a generalized description of the fruit coat can be given for *C. Pepo* and *C. maxima* which closely resemble each other in structural detail. At maturity, the rind of the fruit is hard, while the central hollow portion contains a mass of slimy fibers among which are the numerous flattened seeds. The pericarp and undiverged tissues of the receptacle constitute the bulk of the fruit, including the rind and fibers, and the connecting parenchyma disintegrates before the complete maturation of the fruit.

Barber (2) has divided the pericarp into six distinct regions. The outermost zone (1) consists of prismatic cells that are polygonal in surface view and form a palisade layer, having greatly thickened outer and radial walls with a heavy striated cuticle. The characteristic white spots on the surface, about which the cells are elongated and curved, are stomata from which rows of tangentially elongated cells radiate. The distribution of the stomata is not uniform and occasionally two may be surrounded by the same group of radiating cells. Yasuda (42) has reported a frequency of 44 stomata per square millimeter for *C. Pepo*. Two types of hairs are produced on the epidermal surface, both having basal cells that are somewhat more rounded than the adjacent epidermal cells. These hairs do not persist, but dry up while the fruit is small, leaving the basal cell intact. The large, jointed type is tapering, conical, and multicellular, frequently attaining a length of $1\frac{1}{2}$ to 2 mm. The other is smaller and capitate, consisting of a jointed structure of four or five cells, and a large globular head of one or more cells. (Fig. 308, B.)

The hypodermal zone (2) consists of many layers of small, thick-walled, isodiametric cells with small intercellular spaces. The outer mesocarp (3) lies immediately within the hypodermis and is comprised of cells of graded size, intermediate between those of the hypodermal region and the larger ones of the middle meso-

carp. They are isodiametric with thick walls; and, in the variety *verrucosa*, the region is characterized by many layers of polygonal stone cells. The middle mesocarp (4) is made up of cells which are progressively larger and more loosely arranged than those of the outer mesocarp. The outermost cells contain numerous starch grains, the number decreasing toward the inner limits of this zone.

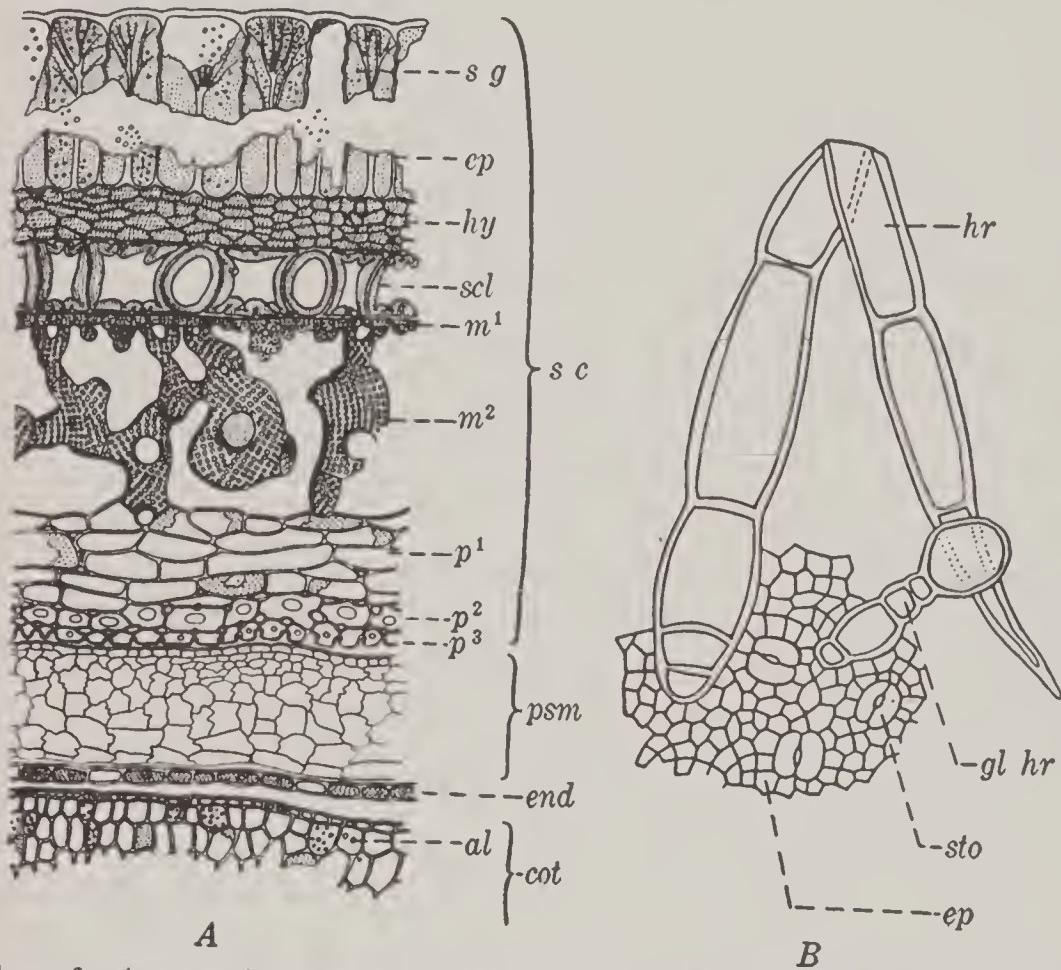


FIG. 308. A, transection of portion of seed of *Cucurbita Pepo*; B, surface view of portion of epicarp of immature fruit showing epidermal hairs: *al*, aleurone grains; *cot*, cotyledon; *end*, endosperm; *ep*, epidermis; *gl br*, glandular capitate hair; *hr*, conical hair; *hy*, pitted subepidermal layer; *m¹*, pitted parenchyma; *m²*, reticulate spongy parenchyma; *p¹*, parenchyma; *p²*, spongy parenchyma; *p³*, inner epidermis of seed coat; *psm*, perisperm; *sc*, seed coat; *scl*, sclerenchyma; *sg*, starch grain; *sto*, stoma. (Redrawn after Barber.)

The inner mesocarp (5) consists of large parenchymatous cells without much cellular contents. Throughout the mesocarp there are vascular bundles and isolated sieve tubes, as well as latex tubes which anastomose with each other. The central portion of the fruit is occupied by tough fibers surrounded by disintegrated parenchymatous cells. The innermost zone or endocarp (6) is made up of very small, thin-walled cells that are tangentially elongated and form a thin membranous tissue which

adheres to the seeds. It becomes firmly attached to the seed coat, but can be separated from dry seeds as a transparent colorless skin.

THE SEED. — The large, flat, ovate seeds are pointed at one end; and vary so definitely in shape, color, margin, and the scar formed at the hilum that Russell (33) has devised a key to separate the three species based on these characters.

The structure of the seed coat has been investigated by Barber (2), Kondo (24), Yasuda (42), and Fickel (10). Kondo investigated that of *C. moschata* and the other accounts described varieties of *C. Pepo*. The seed coat is comprised of five distinct layers of tissue which develop as parts of the two integuments of the anatropous ovule. The outer integument produces the three outermost layers of the seed coat, and a part of the fourth layer; while the remainder of the coat is derived from the inner integument.

The outer epidermis (1) is made up of prismatic cells which form a compact layer, devoid of intercellular spaces. The cells are elongated radially, and those lying at the border form a ridge in which the cells are several times as long as those on the flattened lateral surfaces of the seed. The outer walls of these cells are thickened, but there is little or no cuticle. The radial walls are very thin with characteristic strands of cellulose thickening which extend from the base of the cell and branch frequently toward the outer wall. (Fig. 308, A.)

The subepidermal layer (2) is made up of small, thick-walled, much pitted, polygonal cells that are somewhat elongated. There are no intercellular spaces in this zone, which is three to five layers in thickness except at the margin of the seed where the number increases. The sclerenchymatous region (3) gives firmness to the seed coat, and is one cell layer in thickness except at the margin of the seed where it may be two or three. The longitudinally elongated cells are arranged in rows end to end; and in surface view, the very thick walls appear sinuous with infoldings that overlap one another.

The parenchymatous zone (4) consists of three distinct layers. The outer one is made up of small pitted cells which lie adjacent to the sclerenchyma and have no intercellular spaces. The intermediate region is two layers in thickness and is characteristic of the genus. The intercellular spaces are very large, forming cavities into which the cells project, and the cells are somewhat stellate with walls that have reticulate thickenings. The inner

layers form a true spongy tissue of thin-walled cells, and the innermost layers of this zone are chlorophyllose. The inner epidermis (5) is a layer of small thin-walled cells. (Fig. 308, A.)

Underlying the seed coat is a zone of perisperm or nucellar tissue about six layers in thickness. The cells are thin-walled, except for the outermost one which is epidermal with a definite cuticle. The endosperm consists of a layer of thick-walled cells which have granular contents and large nuclei. The embryo has a short, blunt hypocotyledonary axis from which two flat, somewhat fleshy cotyledons are diverged. A very short conical growing point constitutes the epicotyl.

DEVELOPMENT OF THE SEEDLING. — Owing to the shape of the seed, it lies flat in planting. Under favorable conditions, the primary root protrudes between the halves of the seed coat at the end of two days and extends downward at right angles to the seed. The root grows very rapidly, and may be 3 cm. in length by the end of the third day. At this time the peg begins to develop as a small, lateral, parenchymatous outgrowth in the angle formed by the base of the horizontal hypocotyl and the vertically oriented root. By the fourth day, the peg is enlarged considerably, in some varieties extending part way round the axis; and just below it, the primary root produces many lateral roots. The hypocotyl begins to elongate upward while the cotyledons still remain within the seed coat. This soon splits, since its lower half is held in place by contact with the lower surface of the peg while the upper half is forced open by the growth of the arching hypocotyl. (Fig. 309, A-C.) In some instances, the lower half of the seed coat slips from the peg, and the seed coat is carried above ground, where it is later shed as the cotyledons enlarge.

Eventually, the cotyledons are freed from the seed coat, emerging from the soil; and about the sixth day, the axis becomes erect. The seedling phase is usually completed in seven or eight days, when the primary structures are differentiated, and the reserve foods stored in the cotyledons have been largely utilized. The young plant is then independent, the outspread cotyledons are photosynthetic, and there is a well-branched root system. The growth of the epicotyl is relatively slow during germination; but the first foliage leaf finally develops very close to the cotyledonary plate, since the first internode is extremely short. (Fig. 309, D, E.)

THE PRIMARY Root. — The primary root has a tetrarch, exarch protostele which is surrounded by a pericycle that is uniseriate outside the four primary phloem groups, but may be four or more cells in width at the protoxylem points. (Fig. 310.) The cortical region is limited centripetally by endodermal cells that are vertically elongated, being about equal in length to those of the pericycle. The remainder of the cortex consists of seven to ten layers

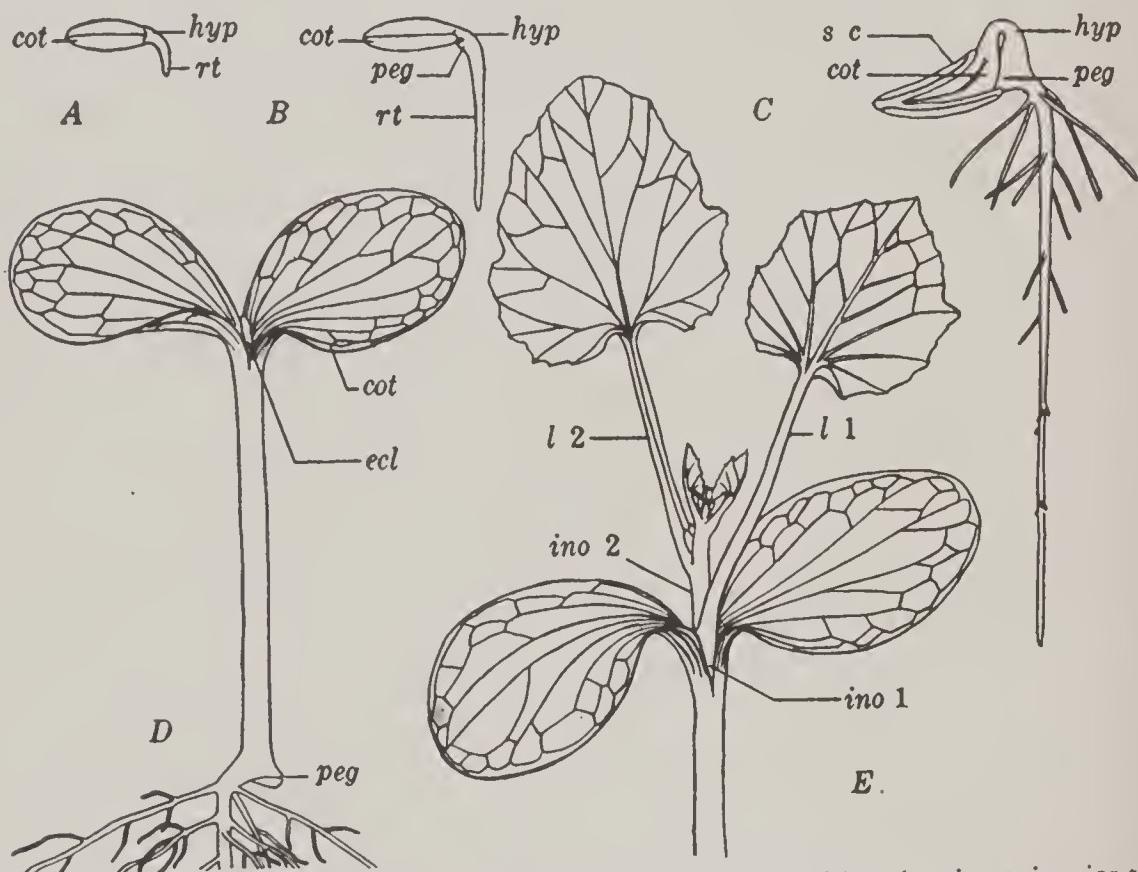


FIG. 309. Stages in development of seedling: A, two-day seedling showing axis prior to formation of peg (seed coat has been removed); B, at three days, showing development of peg; C, same, at five days, illustrating function of peg in splitting seed coat and aiding in withdrawal of cotyledons; D, at eight days, primary growth of seedling is complete; E, older plant showing position of first foliage leaves and relative lengths of first and second internodes: cot, cotyledon; ecl, epicotyl; hyp, hypocotyl; ino 1, first internode; ino 2, second internode; l 1, first foliage leaf; l 2, second foliage leaf; rt, primary root; s c, seed coat. (After Whiting.)

of large parenchymatous cells which are several times as long as wide, and there are conspicuous intercellular spaces. The elongated, tabular epidermal cells are small in radial dimension, and each may form a root hair.

The ontogeny of the root follows Janczewski's (20) fourth type, which is characteristic for the Cucurbitaceae and Leguminosae. In this type, the growing point is not differentiated into distinct histogens; but, instead, the primary tissues of the root axis arise

from a common meristematic zone. Whiting (40), in a study of *Cucurbita maxima*, confirms Janczewski's (20) work and describes this generative zone. The meristem consists of about seven layers of cambiform cells, the number diminishing toward the periphery of the growing point. Terminally, the outermost cells of the generative zone become the cells of the root cap, while the marginal cells function as a dermatogen and produce the epidermis. The joint production of root cap and epidermis by the peripheral portions results in the characteristic "stair-step" arrangement referred to by Janczewski in the description of his third type of root ontogeny. (See Linum, Chapter XIII.)

The remaining tissues are derived from the inner face of the generative zone. The cells undergo several divisions, some of which are irregularly periclinal; and then the centrally located cells differentiate as stelar tissues, while adjacent cells produce the cortical region. In this type, where there is general meristematic activity, it is difficult to follow the differentiation of the various tissues; and the situation is further complicated by the rapid elongation of the root and the delay in the maturation of the primary tissues. It is possible to determine the approximate limits of the cortex and stele relatively early, since the cells of the innermost layer of the cortex continue to divide tangentially for a longer period of time than do the adjacent cells of the stele.

The first stelar tissue to differentiate is the protophloem, which consists of four strands. No sieve tubes develop in the protophloem, which is comprised only of parenchymatous elements that are small in diameter and considerably elongated. In the center of each protophloem group, and usually adjacent to two large pericyclic cells, a single cell differentiates, forming a duct which can be distinguished by its less dense contents. Other

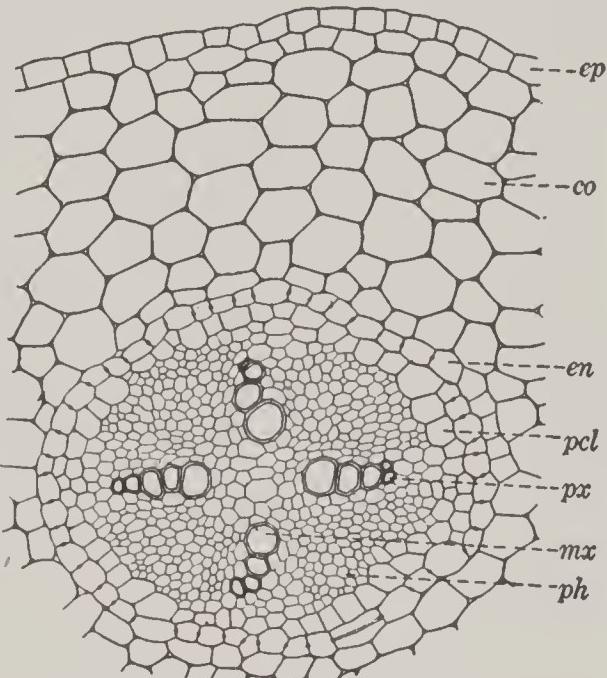


FIG. 310. Transection of sector of young root showing development of xylem prior to differentiation of large central metaxylem: *co*, cortex; *en*, endodermis; *ep*, epidermis; *mx*, metaxylem; *pcl*, pericycle; *ph*, phloem; *px*, protoxylem.

protophloem ducts similar to the initial one may be differentiated adjacent to the pericycle or one or two cell layers removed from it.

The metaphloem develops sieve tubes and companion cells in addition to parenchyma. The sieve tubes are elongated, small in diameter, and have comparatively small sieve plates. The companion cells are nucleate, densely cytoplasmic, and shorter than the sieve tubes so that there may be two or more of them abutting one sieve tube. The major portion of the metaphloem is composed of parenchymatous cells that are larger in diameter than the sieve tubes and usually several times longer than their radial dimension.

The differentiation of the protoxylem parallels the protophloem. The first elements which mature have relatively heavy annular thickenings, and one vessel of this type develops at the outer limit of each protoxylem point. The two or three protoxylem elements centrad to the first formed, annular elements, differentiate as annular or spiral vessels. The relative number of each type is not constant, and occasionally intermediate spiral-annular elements may be formed. The protoxylem vessels soon become stretched and crushed, forming lacunae which may later become conspicuous. The tetrarch pattern of the stele becomes more marked with the progressive differentiation of the metaxylem elements. There are intermediate types between the spiral, reticulate, and scalariform patterns; so that it is difficult to distinguish definitely between the protoxylem and metaxylem. In general, the metaxylem vessels are conspicuously larger than the first formed protoxylem elements, and, for the most part, have closely reticulated thickenings.

Up to this point, the stelar development results in the formation of four radial arms of primary xylem alternating with the four zones of primary phloem, the central portion of the axis remaining parenchymatous. (Fig. 310.) Possibly because of the delayed differentiation of the central portion of the stele, the squash root has been described as having a pith. Van Tieghem (35) and Gérard (12) both mention the presence of a pith; but in the latter case the transection described was probably close to the transition region where a pith is differentiated. Rutledge (34) and Whiting point out that, in *C. maxima*, two or more cells at the center of the stele finally develop to form conspicuously large pitted or reticulate-pitted tracheae. These are surrounded by smaller, isodiametric or horizontally elongated parenchymatous cells which

also have reticulately thickened or pitted walls. (Fig. 312, A.) The centrally located metaxylem vessels with the adjacent thick-walled parenchyma may abut the reticulate vessels of the four primary xylem points; or they may be separated from them by two or three layers of vertically elongated thin-walled xylem parenchyma. (Fig. 312, B.) Between the primary xylem and phloem, there is a zone of parenchyma which later gives rise to the cambium.

As the stele matures, the cortical region is also developing. The inner cortical cells divide periclinally, adding additional layers, and radial divisions occur to compensate for the increased diameter of the stele. Cell divisions cease at about the time that the scalariform elements of the metaxylem develop, and the endodermis then forms narrow Caspary strips.

LATERAL ROOTS. — The lateral and adventitious roots resemble the primary root in structure, but their steles may be triarch or octarch as well as tetrarch. The origin of lateral roots occurs very early in the ontogeny of the primary root when the protophloem is differentiating, and prior to the development of the protoxylem. Whiting observed several root tips in which lateral primordia occurred within a millimeter of the apical meristem. There is some disagreement in regard to the tissues involved in the origin of secondary roots in Cucurbita. According to Janczewski (19), in the ontogeny of lateral roots in Cucurbitaceae and Leguminosae, the stele of the main root gives rise to the stele of the lateral root; while the endodermis and adjacent cortical cells of the main root form the cortex of the lateral root, at the distal surface of which the meristematic growing point is later developed. Van Tieghem and Douliot (38) rejected Janczewski's explanation, stating that in *C. maxima* and *C. Pepo*, there is definite evidence that the lateral root arises from two pericyclic layers, and that the endodermis and five or six of the inner cortical layers produce a digestive pocket which assists in the emergence and the outward growth of the young root. Whiting's studies tend to confirm the observations made by Janczewski. However, the very early initiation of the primordia of the lateral roots, prior to the maturation of the protoxylem and before the endodermal layer of the main root is clearly differentiated, makes it difficult to determine with exactness the location of the tissues from which the primordia arise.

According to Whiting, lateral root formation is first indicated by radial divisions of cells in the two or three inner layers of cortical parenchyma at points centripetal to the protoxylem. (Fig. 311, A.) The radial divisions of the regularly arranged cells of the cortex occur while the innermost layers continue to divide tangentially. At this time, the pericyclic cells begin to divide; and those just centrad to the active cortical region also divide tangentially, with the result that the exact identity of the two adjacent layers is soon lost. Thus, divisions in all three planes account for the formation of the lateral root primordium from cortical and pericyclic tissue.

As additional layers of the cortex are involved, the lateral extent of the root primordium is increased until its base reaches to the phloem on either side of the protoxylem point. (Fig. 311, B, C.) The cortical cells remain meristematic and continue division, but the outline of the mother cell can frequently be traced, even after several divisions have ensued. The regular layered arrangement of the cells in that part of the cortex which is involved in lateral root formation tends to be distorted by the increased activity of the tissues of the pericycle, which by successive divisions produces the numerous small, radially elongated elements of the stele. (Fig. 311, D.)

As the primordium elongates, the cortical cap maintains its position over the stele by divisions of the cells at the base of the primordium and adjacent to the phloem of the parent root. Finally, when all but about three layers of the cortical tissue of the primary root are involved in the root primordium, a meristematic zone similar to that described for the primary root develops. (Fig. 311, D, E.) This is formed by tangential divisions in the second, third, or fourth outermost layers of the cortically derived tissues of the root primordium. As a result of the activity of the apical meristem of the lateral root, its tip is torn away from the cortical tissues of the primary root; and it ultimately penetrates the remaining tissues, emerging into the soil.

THE VASCULAR TRANSITION. — Investigations of the transition by Rutledge (34) and Whiting (40) are in close agreement with the early interpretations of Gérard (12) and Dangeard (6), but differ from that of Lamounette (25). An essential feature of the transition is that, in relation to the number that occurs in the primary root, there is a doubling of the xylem and phloem strands.

There is also a change in the spatial relationship of the proto- and metaxylem, so that the primary xylem matures centrifugally to form endarch strands in the upper limits of the transition, in

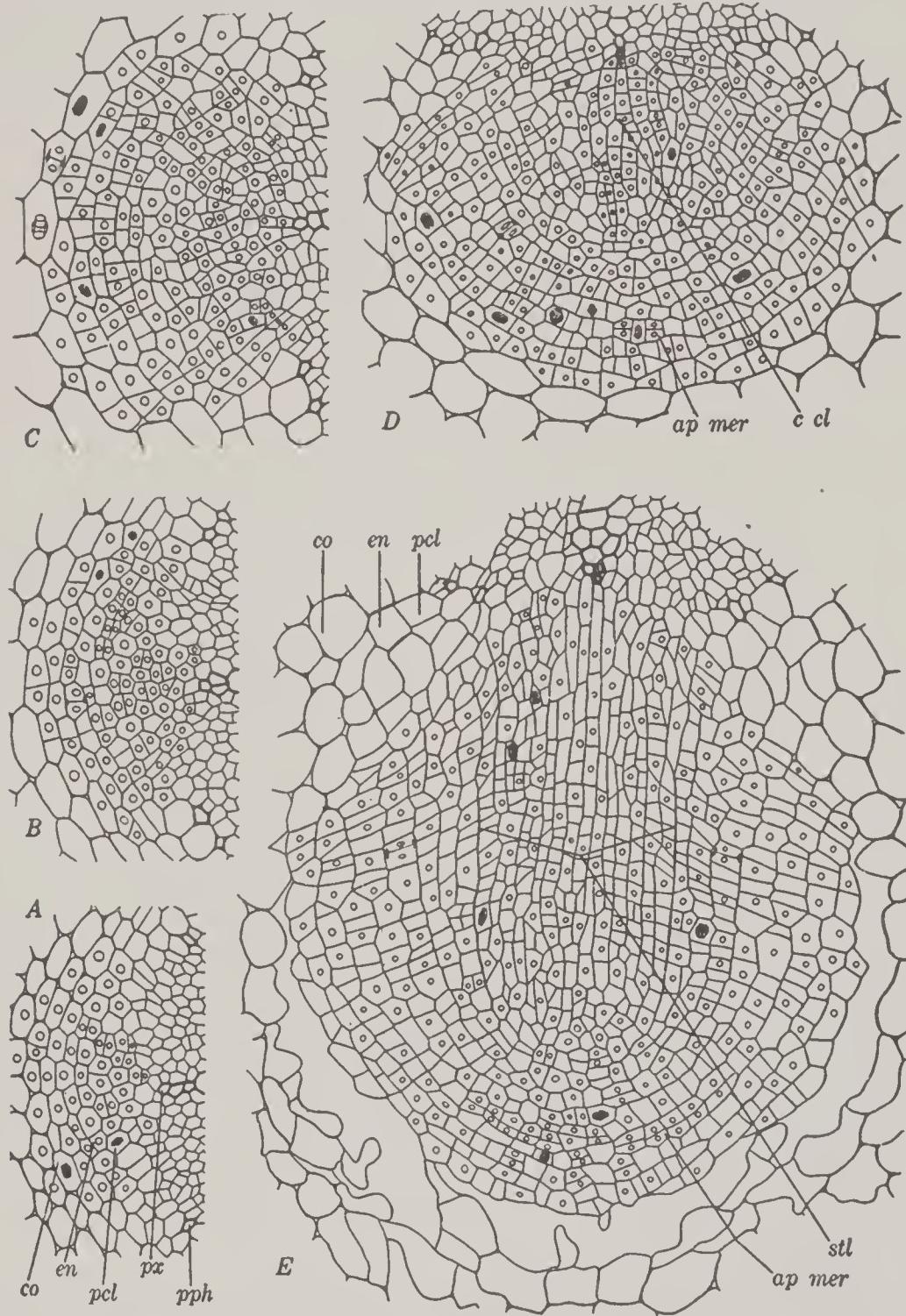


FIG. 311. Transections of portions of primary root showing origin of secondary roots: A, first radial divisions in cortex and tangential divisions in endodermal and outermost pericyclic layers (nucleated cells in region of primordium); B and C, further divisions in cortex and pericycle; D, formation of central cylinder and origin of apical meristem; E, secondary root which has nearly penetrated cortex of primary root with its stele and apical meristem established: *ap mer*, apical meristem; *c cl*, central cylinder; *co*, cortex; *en*, endodermis; *pcl*, pericycle; *pph*, protophloem; *px*, protoxylem; *stl*, stele. (After Whiting.)

contrast to the centripetal development and exarch orientation in the root. The relation of the primary phloem and xylem also shifts from the alternate, radial arrangement to the collateral, which ultimately becomes bicollateral with the development of the inner phloem. In this manner, eight bicollateral bundles are formed, separated by narrow medullary rays. (Fig. 313.)

In *C. maxima*, the transition region extends from a point somewhat below the peg where the axis is exarch and protostelic to a point just above the peg where the vascular tissues form a completely endarch dissected siphonostele. This involves a segment of the axis which is about a centimeter in length in a week-old seedling. The first transitional development is the increase in the number of thickened, parenchymatous cells between the large central vessels. As a result, the pitted vessels are separated into two groups, and the number of large metaxylem vessels is increased to four or more. The narrow band of parenchymatous cells which develops in the intercotyledonary plane increases in width until a definite pith region is formed. (Figs. 312, B, C, and 313, B.)

As the pith develops, the tangentially orientated metaxylem vessels lie in four groups which occupy positions near the periphery of the stele and alternate with the protoxylem points. They are centrad to the four phloem groups and separated from them by several parenchymatous cells which later function as cambial initials. (Fig. 312, C, D.) This is followed by an increase in the number of reticulate vessels, and a lateral development of large pitted metaxylem elements, so that the primary xylem forms a hollow diamond enclosing the pith. (Fig. 313, C.) At higher levels, the reorientation of the stelar tissues is more abrupt; the pith enlarges, and the first inner phloem is differentiated centrad to the xylem triangles formed by the original proto- and metaxylem. (Figs. 312, E, and 313, D.) The cells of the inner phloem have end walls that are perforated, and they resemble the sieve tubes of the outer phloem except that they are much larger.

A millimeter or two higher, each protoxylem point divides and the halves are separated by parenchymatous rays. (Fig. 313, F.) Thus, a dissected siphonostele of four transition bundles is formed, each consisting of a tangential band of metaxylem terminated at both ends by annular and spiral protoxylem elements with the primary phloem lying in a position collateral to it. The metaxylem of the bundle consists of small reticulate tracheae, and

two or more larger, later-maturing, pitted vessels which lie on the outer face of the tangential band. (Fig. 314, A.) The inner

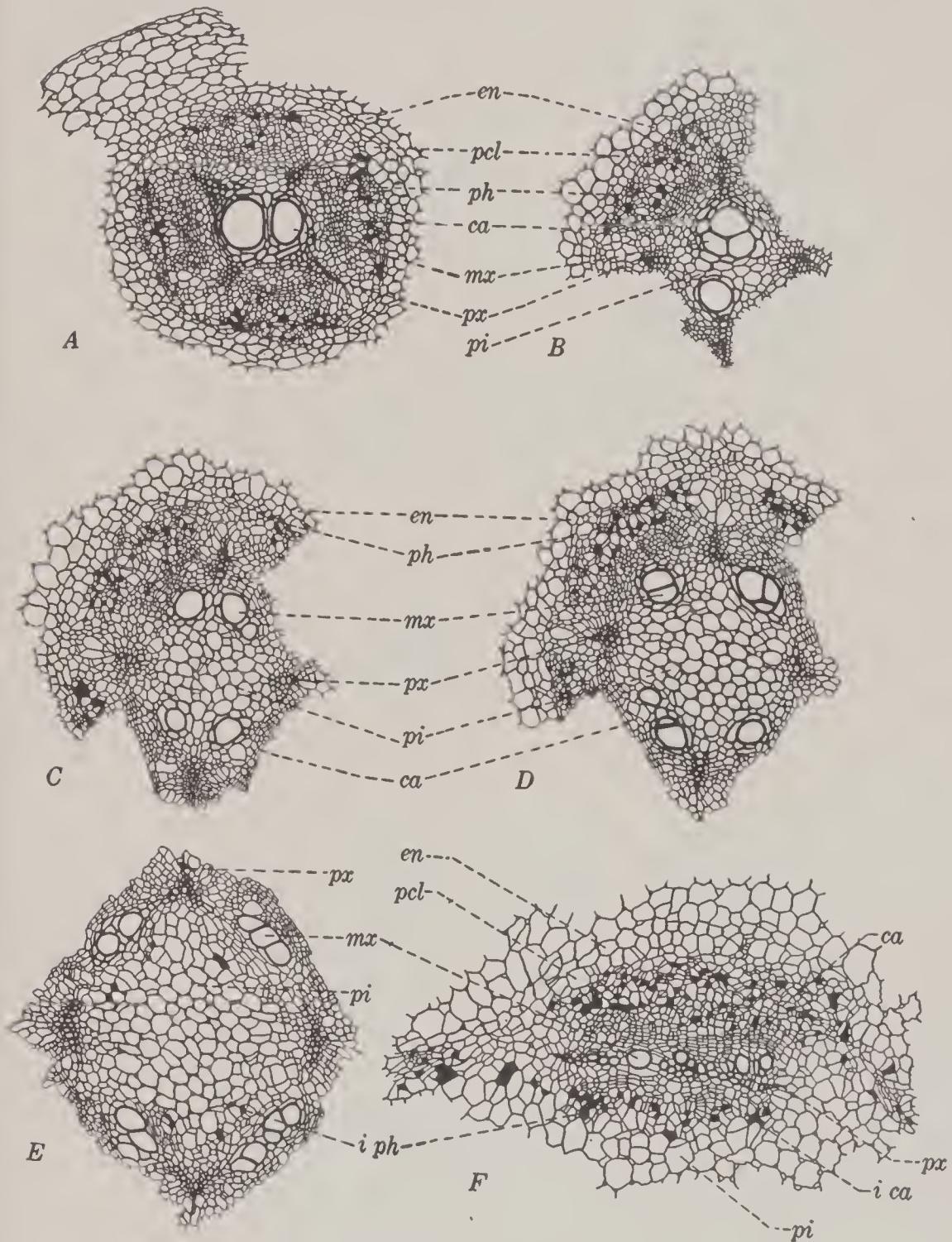


FIG. 312. A-F, transections of sectors of root and hypocotyl showing stages in vascular transition: A, upper level of primary root; B, lower hypocotyl showing pith; C, 4 mm. above B; D, hypocotyl about 2 mm. above C in which inner cambium is forming; E, about 2.5 above D in which metaxylem groups are bifurcated and there is a definite inner cambium and inner phloem; F, one of transition bundles showing lateral position of protoxylem, inner cambium, inner phloem, interfascicular phloem and some of connective phloem cells: ca, cambium; en, endodermis; i ca, inner cambium; i ph, inner phloem; mx, metaxylem; pcl, pericycle; ph, phloem; pi, pith; px, protoxylem. (After Rutledge.)

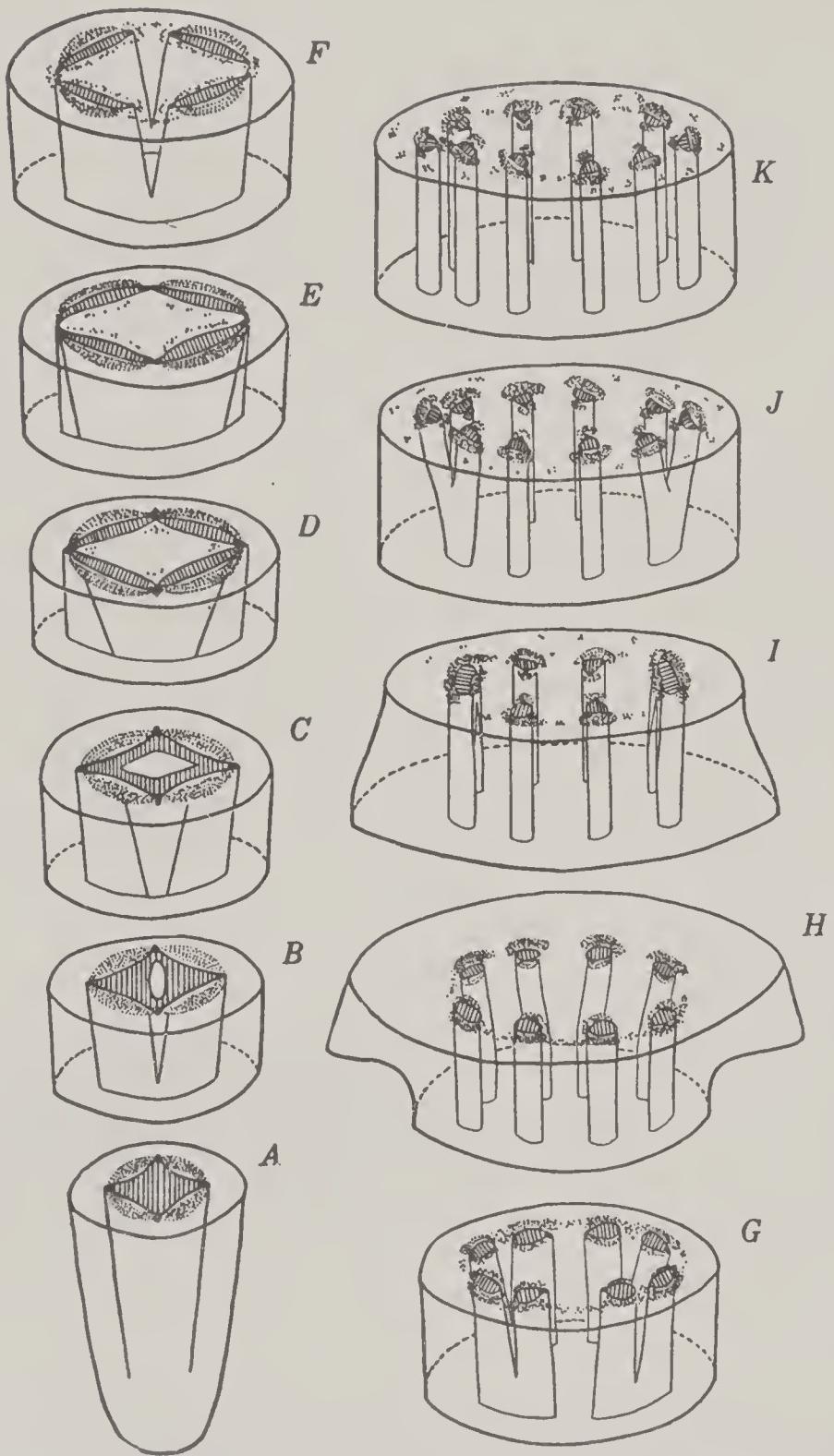
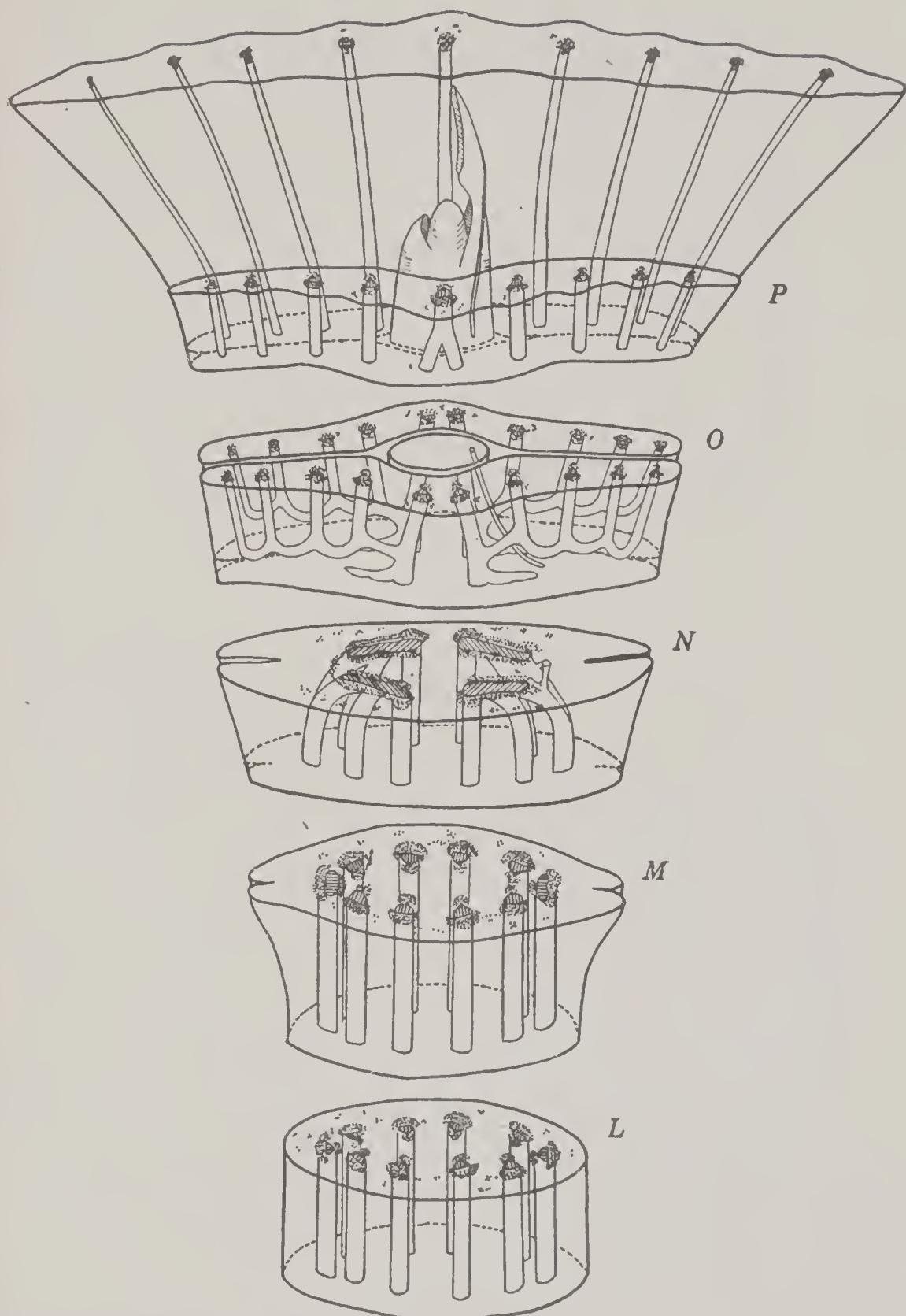


FIG. 313. Vascular transition. Series of transections showing: *A*, root; *B*, differentiation of pith; *C*, enlargement of pith area with metaxylem in peripheral position; *D*, differentiation of inner phloem; *E*, tangential divergence of each primary xylem strand; *F*, establishment of dissected siphonostele of four, tangential, transition bundles; *G*, formation of eight bundles, each with protoxylem in tangential position; *H*, abrupt enlargement of axis at peg,



with primary xylem becoming endarch; *I*, endarch bundles completing transition, anastomosing of two end pairs of bundles; *J*, end bundles dividing into three to form ten bundles which continue through hypocotyl; *K-P*, vascular anatomy of cotyledons, *P* showing epicotyl. Stippled regions indicate phloem; lined regions, metaxylem; and solid black ones, protoxylem. (After Whiting.)

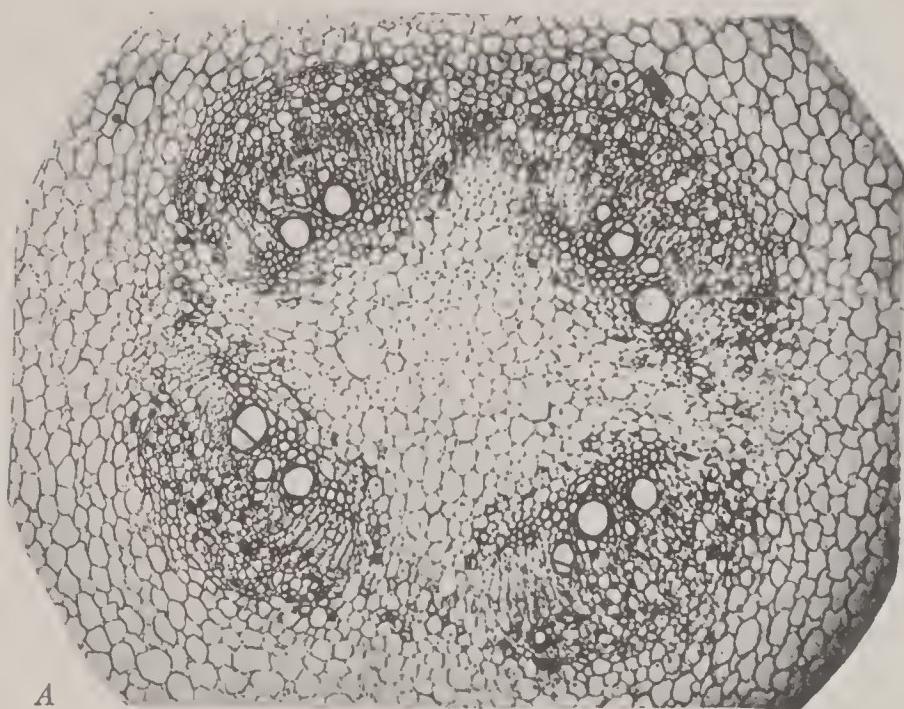
phloem forms a zone on the centrad face of each bundle, but is interrupted by the four rays. The outer phloem is continuous with that of the root, having maintained its original position. There is often a differentiation of phloem across the rays connecting the adjacent areas of outer phloem; also a development of connective phloem in the ray, which establishes continuity between the inner and outer phloem groups of each bundle. (Fig. 312, F.)

The diameter of the axis increases in the region of the peg, the pith becomes larger, the bundles are separated by wider rays, and their number is increased from four to eight. (Fig. 313, G, H.) These are transitional, since the metaxylem is still tangentially oriented in relation to the protoxylem, except that a few large pitted vessels are located on the outer face of the first-formed elements in an endarch relationship. (Fig. 314, A.) The inner phloem is separated from the xylem by one or two layers of parenchymatous cells which may or may not initiate cambial activity, and this situation also obtains in the zone between the lateral phloem and the vascular tissue. The pericyclic zone is irregularly multi-layered, the endodermis persists as a continuous uniseriate layer, and root hairs develop approximately to the peg.

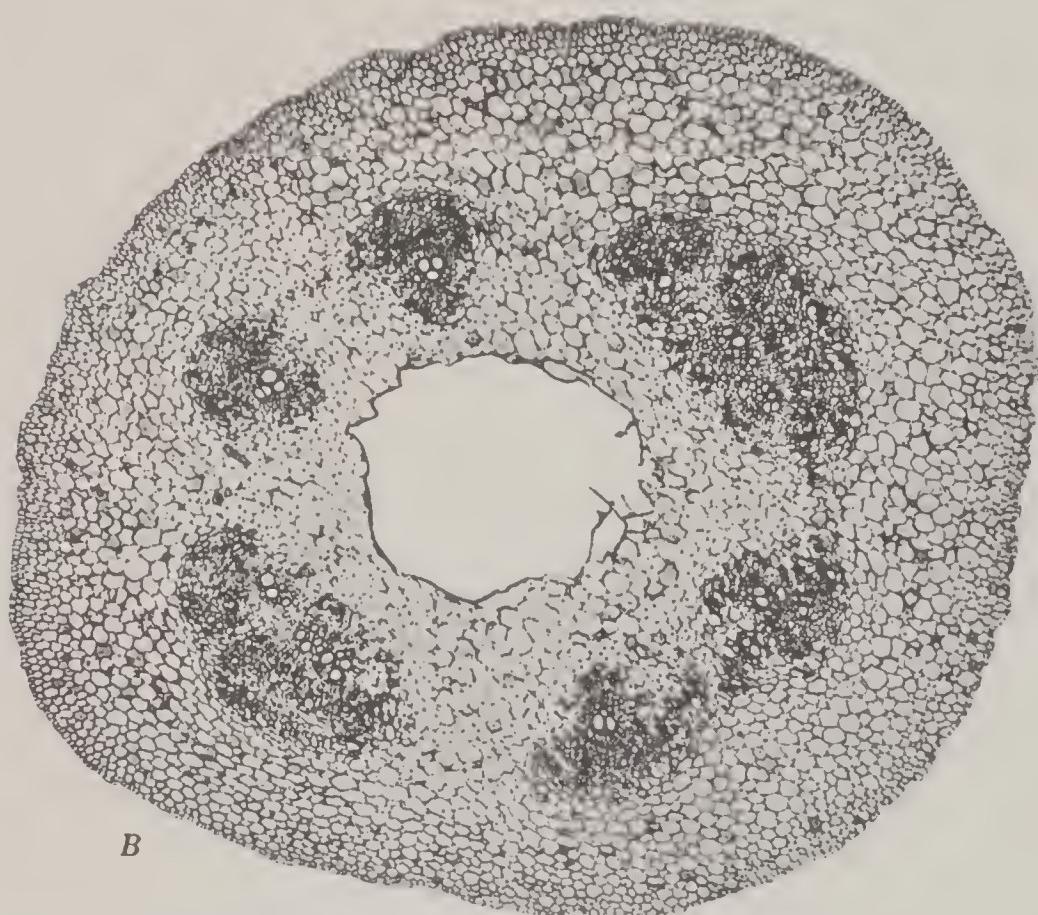
In the upper portion of the peg, the primary xylem develops in an endarch relationship rather than tangentially. (Fig. 313, I.) This is accompanied by a change in the metaxylem elements, which, instead of being scalariform and reticulate, as in the root, are chiefly spiral or loosely scalariform and somewhat larger in diameter. There is also a greater continuity of the phloem, the outer strand forming a broad mass capping each bundle, while the inner one maintains its centrad position.

THE PEG. — Although the transition occurs in the axis at the point where the peg develops, there seems to be no constant relationship between the transition and the structure of the peg. Whiting points out that in some cases the greatest dimension of the peg occurs at the level where there are four tangential transition bundles; while, in other instances, the maximum diameter of the peg is at the point where there are eight or more endarch bundles. The pattern of transition is determined in the embryo at a time when there is no evidence of an enlargement to form the peg, and this structure does not begin to develop as a lateral ridge until about the third day after planting.

The anatomy of the peg is simple, and its growth results from



A



B

FIG. 314. The transition region: A, dissected siphonostele with four transition bundles, each with a tangential band of metaxylem terminated at either end by protoxylem; the outer phloem masses are joined across rays by connective phloem, and inner phloem is continuous with outer phloem; B, complete endarch bundles in region just above peg. One of anastomosed end bundles is branching. (Photomicrographs by Whiting.)

numerous cambial-like divisions which occur in a plane extending tangentially across the axis. In the peg, the greatest dimension of each parenchymatous cell is the radial one; while in other parts of the hypocotyl, the long axes of the cells are in the vertical plane. At the lower limits of the peg, this activity is usually cortical; but in the upper part, the divisions may also involve the stelar tissues which accounts for the abrupt outward divergence in the course of the bundles at this level. The broad lower face of the peg may bear root hairs and is oriented at right angles to the axis; or, less frequently, at an acute angle to it. The upper part of the peg merges gradually into the hypocotyl and has the same smooth cutinized epidermis characteristic of the latter. Above this point, the epidermis produces hairs and stomata, the latter occurring in a frequency of about 20 to 25 per sq. mm.

Crocker, Knight, and Roberts (5) state that the development of the peg is related to external factors which are concerned with the arching of the hypocotyl, the contact of the seed coats, and gravity. They express the opinion that there is no evidence that gravity acts as a direct stimulus to the lateral placement of the peg; and that

"Contact of the coats is by far the more effective for it will induce very sharp arching even against gravity. . . . Arching leads to an increased development of the peg, as well as to its lateral placement, and in many cases produces a peg where it would not otherwise appear as in Big Tom. Contact likewise increases the size of the peg independent of its effect through arch production."

THE HYPOCOTYL. — The peg is at the base of the oval hypocotyl which continues this configuration to the cotyledonary node, the long axis being in the vertical plane of the cotyledons. The course and number of the bundles in the hypocotyl is variable. The eight original bundles are arranged two at each end of the oval and two along each side (Fig. 313, *H*); but, usually, the number increases just above the level of the peg. This is accompanied by branching and anastomoses of the eight bundles, so that they may vary from 10 to as many as 16, the most common number being 10 or 12. (Fig. 314, *B*.)

In the upper portion of the transition zone, the two bundles at each end of the oval anastomose, and each of the resulting large bundles continues up the axis for a short distance and then is divided to form three bundles. (Fig. 313, *I, J*.) These six,

together with the two on each lateral face, make up the basic number of 10 bundles. Frequently, an additional one is formed on each side of the oval by the branching of one or the other of the lateral bundles. (Fig. 315, A.) The bundles so derived continue up the axis to the cotyledonary node; but any of them may give rise to one or more additional bundles, this being especially true of those located at the ends of the oval. (Fig. 313, I-M.)

THE COTYLEDONARY NODE. — At the cotyledonary node, the divergence of the cotyledons results in the formation of a complicated vascular pattern which, like that of the hypocotyl, may show many variations. About 3 or 4 mm. below the node, the middle bundle at each end of the oval divides into two parts which separate and anastomose with adjacent lateral bundles. These continue in a tangential course until each end bundle anastomoses with its respective adjacent central bundle, reducing the number of bundles to four, two in the center of each broad side of the hypocotyl. (Fig. 313, N.) The upward continuations of these four bundles connect with the traces of the cotyledons. The four traces continue upward and outward into the broad bases of the cotyledons; but before the divergence of the cotyledons is complete, each trace branches laterally so that a single vascular bundle differentiates toward the margin of the cotyledon. (Fig. 313, O.) From this lateral vein, four or more large veins diverge upward, and the two median traces also continue into the cotyledon where they may anastomose to form a single median vein or remain distinct. Thus, the vascular system of each cotyledon consists of at least nine principal vascular bundles. (Fig. 313, P.)

An inner or adaxial phloem is present in the veins; and, in the larger ones, connective phloem is also differentiated. Along the adaxial surface of the vascular bundles there are zones of collenchyma, and the mesophyll is 15 or more cell layers in thickness. The three adaxial ones form a closely arranged palisade region, and the remaining 12 or more comprise the spongy parenchyma, which has some intercellular spaces. The cells of the upper epidermis are somewhat larger than those of the lower and may develop multicellular hairs, while the lower surface is glabrous. Stomata occur in both surfaces with about equal frequency, Yasuda (42) reporting 224 per sq. mm. in the upper, and 253 in the lower for *C. Pepo*.

THE EPICOTYL. — At the time of germination, the epicotyl consists of a small growing point covered by the primordium of the

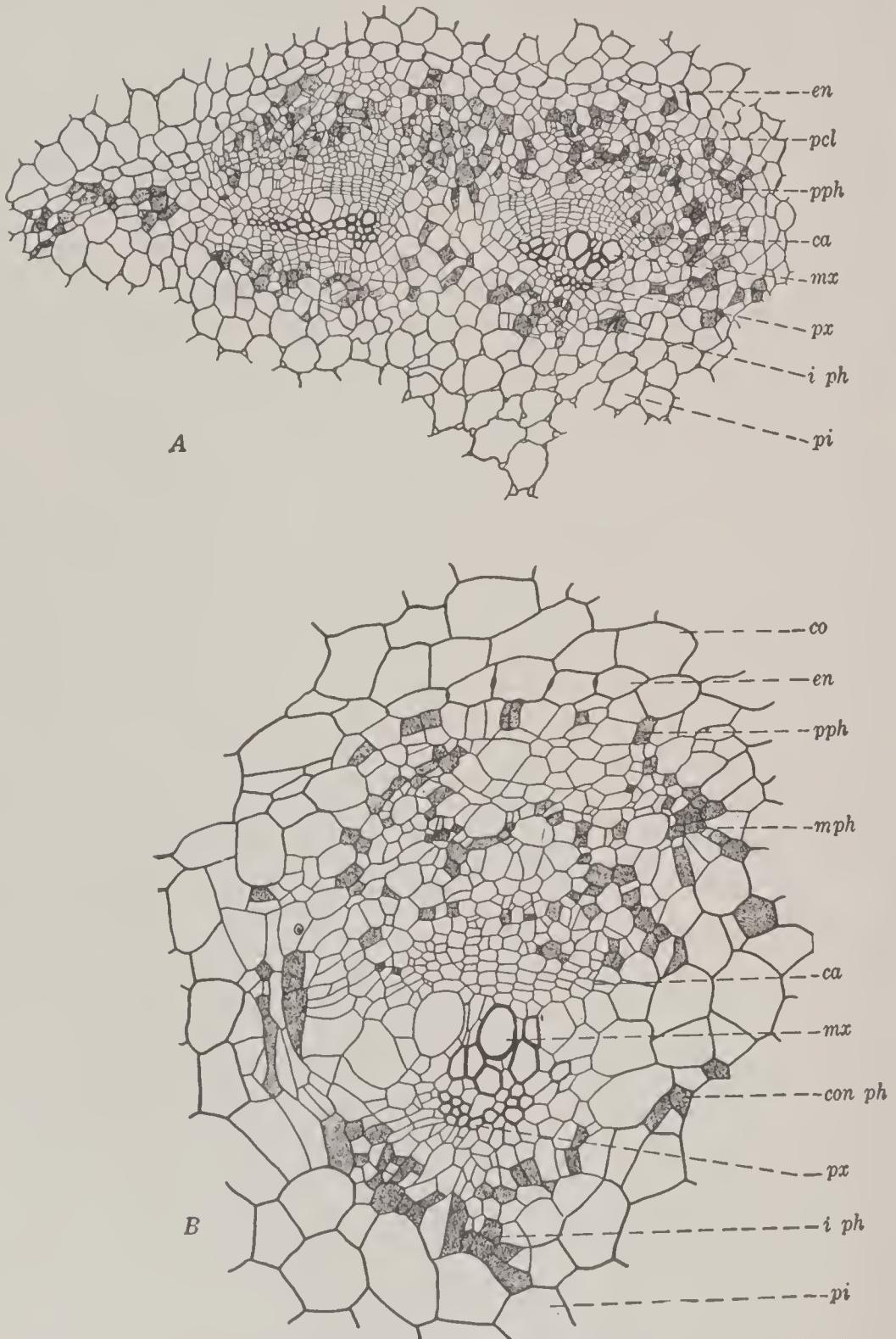


FIG. 315. *A*, transection in upper transition region showing two bundles formed by branching of one transition bundle. The bundle at right is essentially endarch, but protophloem of other bundle is at one side; *B*, transection a short distance above transition showing bundle with connecting phloem strands and absence of inner cambium: *ca*, cambium; *co*, cortex; *con ph*, connective phloem; *en*, endodermis; *i ph*, inner phloem; *mph*, metaphloem; *mx*, metaxylem; *pcl*, pericycle; *pi*, pith; *pph*, protophloem; *px*, protoxylem. (After Rutledge.)

first leaf. After a week, as many as six leaves may be differentiated, but the entire structure is still small and enclosed by the bases of the two cotyledons. (Fig. 309, D.) In about two weeks, the first leaf expands, being diverged at right angles to the plane of the cotyledons.

The bundle supplying the first leaf usually anastomoses with one or two branches of the cotyledonary trace; and the other epicotyledonary traces are later differentiated against the transverse bundles of the cotyledonary plate. The number of bundles and their arrangement in the first internode are variable; but in the second and third internodes, the two cycles of bundles are established which characterize the upper internodes.

THE BICOLLATERAL BUNDLE. — Since Hartig (15) described the occurrence of inner phloem in *C. Pepo* in 1854, there have been many investigations of the vascular relationships that exist in the Cucurbitaceae. Because differences in the interpretation of the phloem have arisen, a brief summation of the divergent views is here included. De Bary (3) originated the term "bicollateral" to apply to vascular bundles which have

"two groups of phloem one being situated . . . on the outside of the xylem and a second on its inner side."

He pointed out that

"both groups of phloem have the typical structure . . . and are especially remarkable for the size of their sieve tubes. They are frequently connected by means of a narrow band, fringing the lateral edge of the bundle, and containing some sieve tubes, so that in these cases the bundle, strictly speaking, belongs to the concentric type." (Fig. 315, B.)

Héral (17) agreed with de Bary, interpreting the bundle as truly bicollateral, since he found the development of all three parts — outer phloem, xylem, inner phloem — to be synchronous. Von Faber (9) concluded that both the inner and outer phloem were similar in structure, arising from a single procambial strand, and regarded the term "bicollateral" as accurately describing the bundle.

On the other hand, Lamounette (25) thought that the inner phloem developed subsequently to the outer, being formed by the activity of parenchymatous cells in the medulla. He observed no inter-connection between the two and advocated the abandonment

of the designation "bicollateral." Baranetsky (1) regarded the inner phloem as of independent origin, and Worsdell (41) stated that "the medullary phloem represents, probably in all cases, a vestigial structure, the remnant of a former system of medullary vascular bundles in which the xylem has disappeared."

With respect to the interconnection of inner and outer phloem, there has also been some difference of opinion. Gérard (12) traced the course of the bundles in the root and stem, finding that the inner phloem consists of branches from the outer. Fischer (11) stated that, in the transition region, the inner phloem ends blindly at its lower extremity; but distinguished four kinds of phloem, one called commissural because it connects the other types. The three categories in addition to commissural phloem are: (1) hypodermal or ectocyclic phloem, occurring between the epidermis and the stele; (2) fascicular phloem, an integral part of the bundle; and (3) entocyclic phloem, formed within the stele. Holroyd (18) adopted the terminology of Fischer, attributing the origin of the internal, or entocyclic, phloem to the development of what he designated "perixylary" cambium, stating that "through immediate activity of the inner cells of this cambium . . . patches of internal phloem originate in front of each bundle."

Whiting has investigated the situation in *C. maxima* in connection with the ontogeny of the hypocotyledonary bundle. The provascular strand at first consists of small elongated cells without intercellular spaces. (Fig. 316, A.) The annular or loosely spiral protoxylem elements develop first; but they do not arise at the extreme inner margin of the procambial strand, one or more of the centrad layers remaining undifferentiated. The outer protophloem is formed at the same time, followed by the metaphloem, which consists of sieve tubes and companion cells that can be identified in seedlings five days old. (Fig. 316, B.) By the sixth day, the small protophloem cells are crushed and resorbed; and, in the meantime, the inner phloem differentiates in the procambial tissue on the centrad margin of the provascular strand, forming sieve tubes and companion cells similar to those of the outer metaphloem.

The development of the inner phloem is centripetal, and a zone of undifferentiated parenchyma remains between it and the primary xylem. In this region, the inner cambium arises later in ontogeny, but it remains inactive during the primary growth. (Fig. 316, C.)

This and other investigations indicate that the vascular bundle of the Cucurbitaceae should be regarded as strictly bicollateral, if the criteria for that type as outlined by Hérail (17) are accepted. These are the differentiation of the inner phloem from the pro-

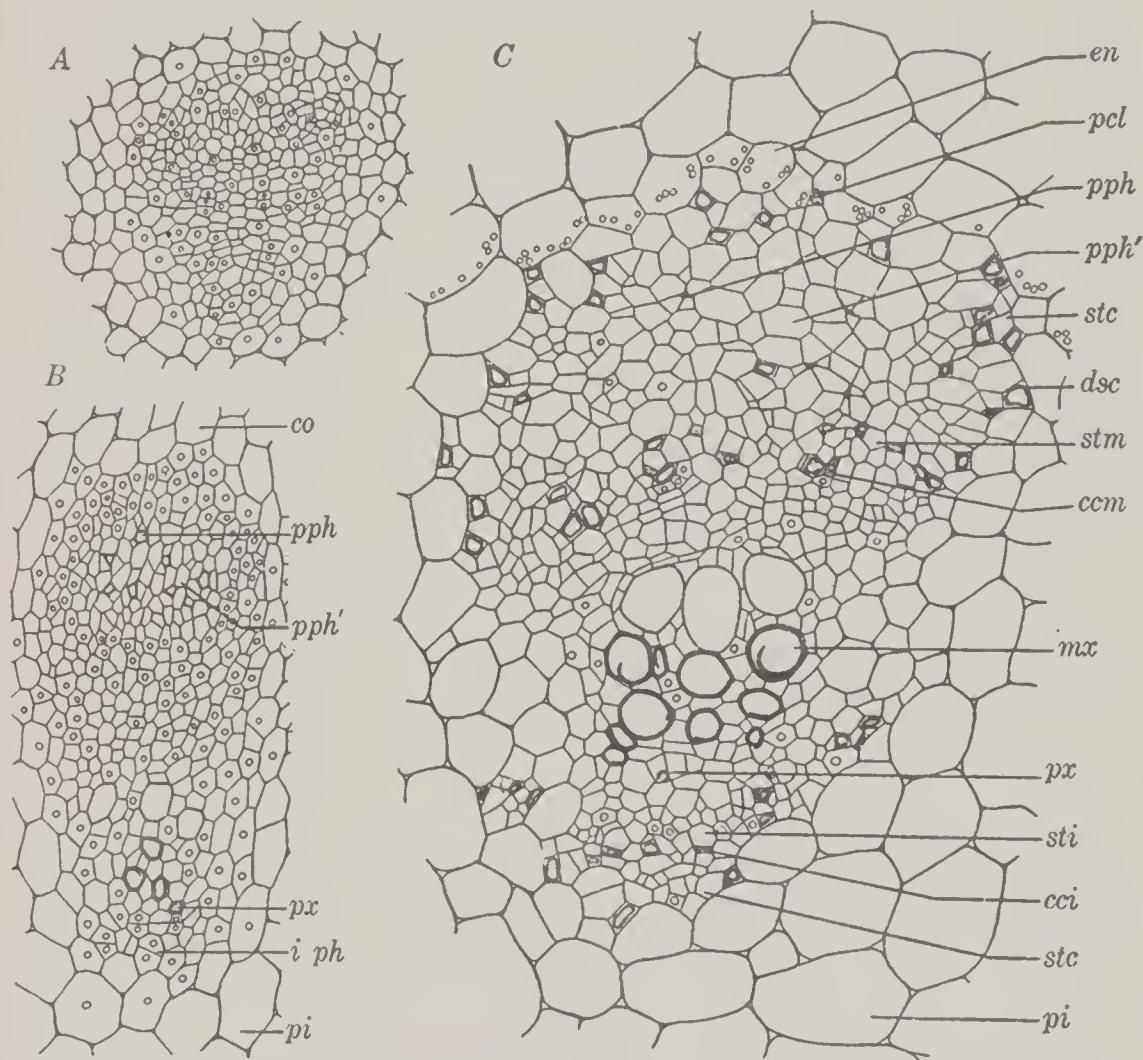


FIG. 316. Transections showing stages in differentiation of hypocotyledonary vascular bundle: *A*, provascular strand in embryo just prior to germination; *B*, vascular bundle of three-day seedling showing development of outer protophloem; *C*, vascular bundle of seven-day seedling in which primary differentiation is nearly complete, with crushed protophloem elements, fibers, metaphloem, inner phloem, and connective phloem which is conspicuous because of dark staining cells: *cci*, companion cells of inner phloem; *ccm*, companion cells of metaphloem; *co*, cortex; *dsc*, dark staining cells in connective phloem; *en*, endodermis; *i ph*, inner phloem; *mx*, metaxylem; *pcl*, pericycle; *pi*, pith; *pph*, protophloem; *pph'*, parenchyma cells of protophloem; *px*, protoxylem; *stc*, sieve tubes of connective phloem; *sti*, sieve tubes of inner phloem; *stm*, sieve tubes of metaphloem. (After Whiting.)

cambial strand and the simultaneous development of the inner and outer phloem.

SECONDARY THICKENING OF THE ROOT. — Secondary thickening of the root is initiated by the differentiation of a cambium in the zone of fundamental parenchyma between the primary xylem and

phloem. The secondary tissues appear in transection as four large wedge-shaped sectors that are separated from one another by prominent rays formed by the continued activity of the pericyclic cells. (Fig. 317.) These may be interpreted as pericyclic rather than secondary xylem rays, since the cambium is confined to the four sectors of vascular tissue. As secondary thickening proceeds, the cortical and epidermal tissues are split; but the pericyclic region continues to keep pace with cambial activity, maintaining itself as a multi-layered zone outside of the secondary phloem and producing a phellogen which forms the protective periderm.

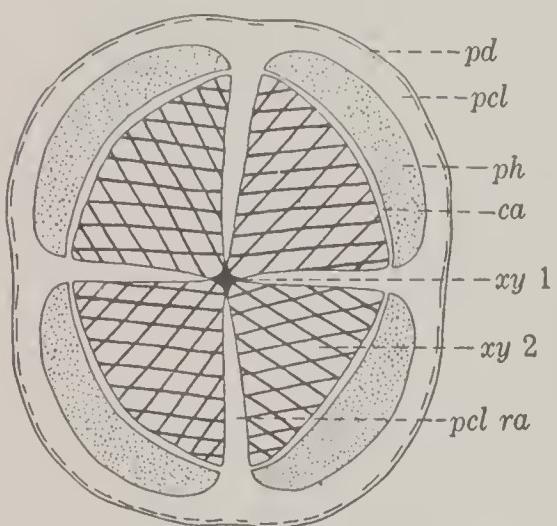


FIG. 317. Diagrammatic transection of mature root: *ca*, cambium; *pcl*, pericycle; *pcl ra*, pericyclic ray; *pd*, periderm; *ph*, phloem; *xy 1*, primary xylem strand; *xy 2*, secondary xylem.

vessels as a result of the intrusion of bladder-like projections of adjacent parenchymatous cells through the pits. These sac-like protrusions contain cytoplasm and usually a nucleus, and the introduction of several such processes, together with their further division, frequently results in the complete filling of the vessel with tyloses that become flattened by reciprocal pressure. (Fig. 318.)

The large size attained by the vessels throws them out of a regular radial alignment, so that they appear as scattered units distributed through each of the xylem wedges. The fibers are long and slender with tapering ends and their number and arrangement may vary. In some cases, the secondary xylem consists largely of fibers and tracheids surrounding the vessels; in others, the fibers occur only in small groups; but in most instances, each vessel is nearly enclosed by tracheids which are separated from it by a zone of

The secondary xylem consists of large vessels, tracheids, fibers, and small isodiametric parenchymatous cells which surround the vessels and are connected with them by simple or half-bordered pits. The short vessel segments are very wide, in some cases being 0.5 mm. in diameter; and in the ontogeny of the vessel, the end walls of a series of segments are digested so as to form a continuous trachea. (Fig. 10.) Tyloses occur frequently in the older

parenchyma. The number and distribution of the parenchymatous cells are also variable, but they are usually more numerous in the

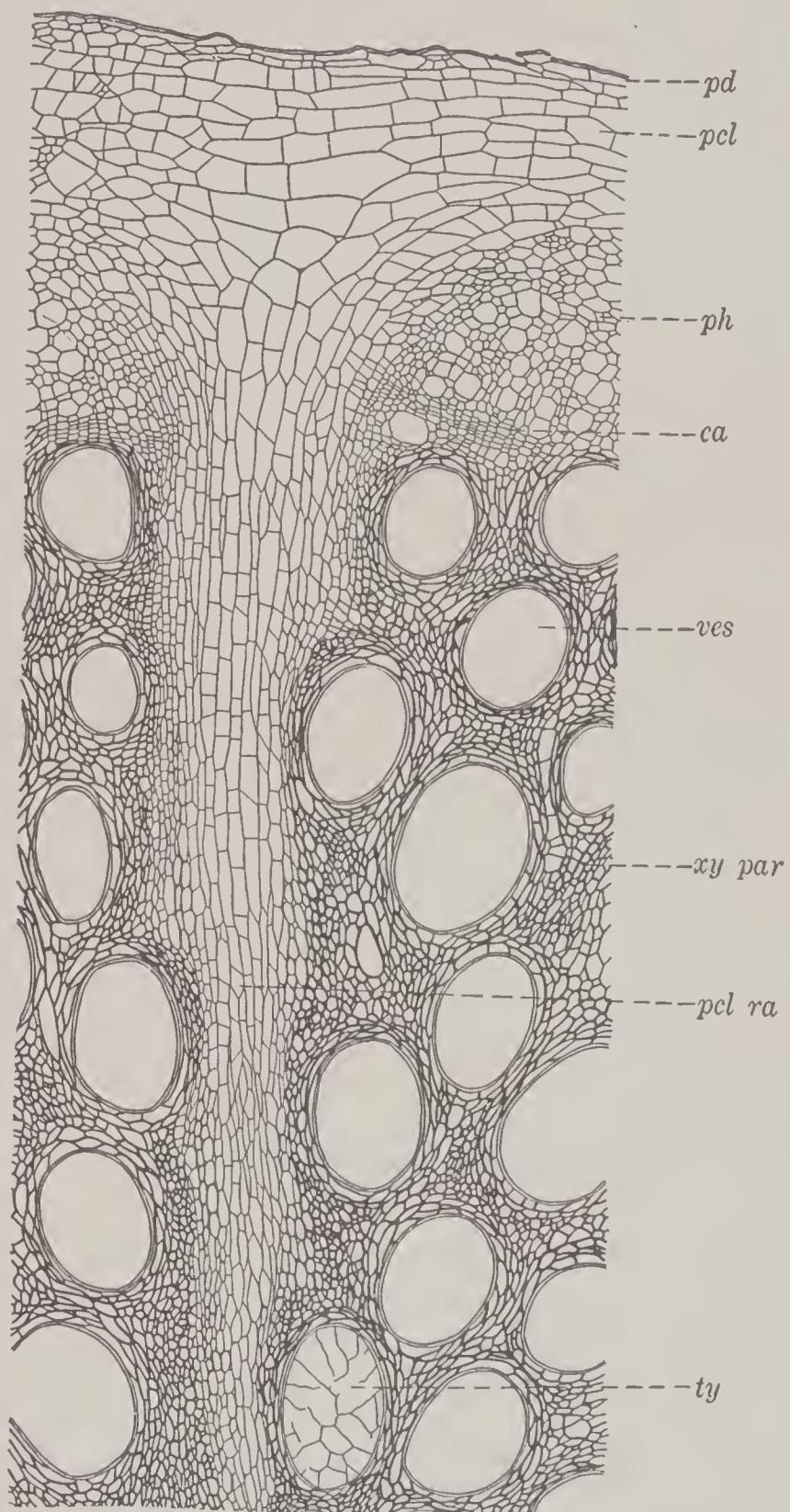


FIG. 318. Transection of sector of mature root showing ray and secondary tissues: *ca*, cambium; *pcl*, pericycle; *pcl ra*, pericyclic ray; *pd*, periderm; *ph*, phloem; *ty*, tyloses; *ves*, secondary xylem vessel; *xy par*, xylem parenchyma.

peripheral portion of the secondary xylem. They are small and isodiametric except that those adjacent to the vessels are stretched periclinally. Occasionally, the sectors of secondary xylem may be partially segmented by xylem rays of thin-walled parenchyma which extend about half way to the center of the axis.

The total amount of secondary phloem produced is not large as compared with the secondary xylem. It occupies four zones outside the secondary xylem, the groups being separated from each other and bounded externally by pericyclic tissue. The sieve tubes are among the largest known, attaining an average diameter of 0.05 mm., and Yasuda (42) has reported a width of 0.067 mm. for *C. Pepo*. The sieve plates have very large pores located in the horizontal or slightly inclined end walls. The companion cells are relatively large, and there may be three or four of them in a linear series adjacent to a single sieve tube.

SECONDARY THICKENING OF THE HYPOCOTYL. — Above the transition region where the bundles are strictly endarch, secondary thickening is initiated in the usual manner, and the fascicular cambium in each of the ten or more bundles produces secondary xylem and phloem elements similar to those described for the root. As the stele enlarges, the ray and pericyclic tissues keep pace so that the bundles are separated from each other by parenchymatous tissue. The outer phloem is limited outwardly by the persistent pericycle, which forms a cap of fibers. The cortex and epidermis persist longer than in the root but ultimately disintegrate and a phellogen of pericyclic origin produces a periderm. The medullary parenchyma also disintegrates so that the hypocotyl is hollow at maturity.

The inner cambium becomes active soon after the outer one, producing phloem elements centripetally and parenchymatous cells centrifugally. (Fig. 319.) As Holroyd (18) has pointed out, the outer cambium of each bundle may become continuous with the inner cambium around the lateral and anterior faces of each bundle, forming what he terms "perixylary" cambium. From the inner cells of this cambium, strands of inner phloem originate centrad to each bundle. The growth of the inner phloem is somewhat variable; and, since the inner cambium also cuts off parenchymatous cells in large numbers, the phloem strands in old hypocotyls are frequently separated from the protoxylem of the bundle by a wide zone of parenchyma. In some cases, this may become

active and produce strands of phloem adjacent to the primary xylem. (Fig. 319.) The lateral sectors of the perixylary cambium remain inactive for some time, but later produce groups of phloem which extend tangentially from the flanks of the meta- and secondary xylem of the bundle.

As the hypocotyl matures, the radial elongation of the parenchymatous cells separating the inner phloem from the protoxylem

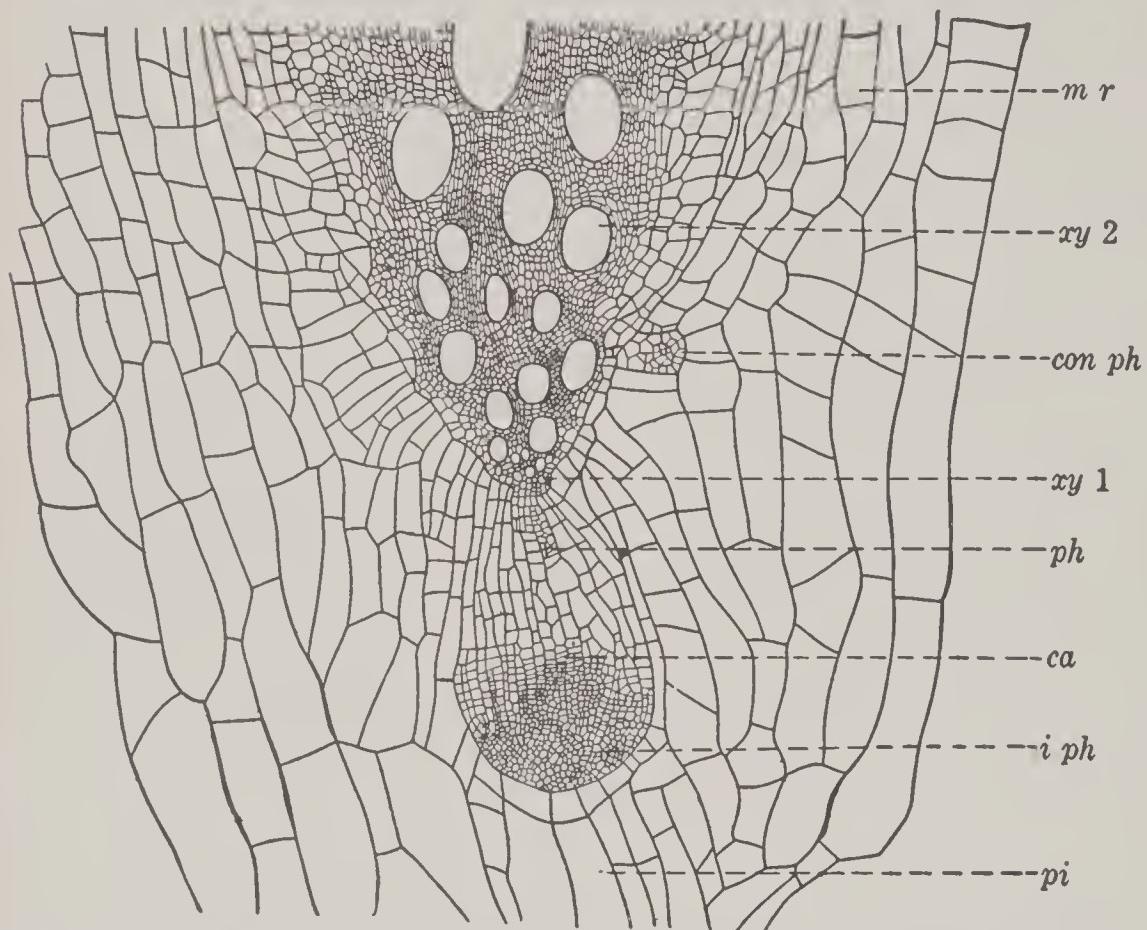


FIG. 319. Transection of centrad portion of hypocotyledonary bundle showing development of inner and connective phloem: *ca*, inner cambium; *con ph*, connective phloem; *i ph*, inner phloem; *mr*, medullary ray; *ph*, phloem; *pi*, pith; *xy 1*, primary xylem; *xy 2*, secondary xylem.

increases the interval between the two, and the inner cambium may cut off some xylem elements centrifugally, forming an obcolateral bundle. In addition to the phloem produced by the outer, inner, and perixylary cambiums, a limited amount of intraxylary phloem may be produced in the xylem parenchyma. This has been noted by Holroyd (18) in *C. Pepo*, and by Rutledge (34) in *C. maxima*. The situation with respect to the phloem is further complicated by the fact that strands of ectocyclic phloem are originated in the pericycle outside the bundles, and also in the

ray regions. All of these phloem types are interconnected by strands of connective phloem, so that this diverse and complex system may be regarded as having continuity although some of the elements end blindly in parenchymatous tissue at various points in the axis.

THE STEM. — The vascular bundles of the stem are arranged in two rings. The smaller ones of the outer ring are located at the angles of the stem, and the larger bundles of the inner ring are alternate with those of the outer. (Fig. 320.) The basic number of bundles is ten, each cycle consisting of five, although occasionally additional smaller ones may be present. All the bundles are common, and the bi-cyclic character of the dictyostele is related to the mode of insertion and downward divergence of the traces of the leaf. Each vascular strand extends downward through the stem for an average of

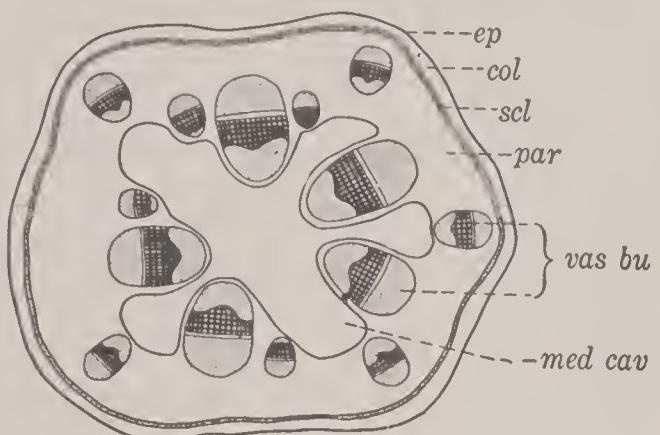


FIG. 320. Diagrammatic transection of stem showing distribution of bundles: *col*, collenchyma; *ep*, epidermis; *med cav*, medullary cavity; *par*, parenchyma; *scl*, sclerenchyma; *vas bu*, vascular bundles.

two internodes before anastomosing with another bundle. Within the inner ring, the pith becomes disintegrated, and a large irregularly shaped cavity is formed.

Outside the outer ring of bundles and continuous with the medulla is a broad zone of parenchymatous tissue. This is limited externally by an uninterrupted band of sclerenchyma five or more cell layers in width; but the continuity may be broken in old stems by secondary growth. (Fig. 321.) The parenchyma and the adjacent fibers together constitute the pericyclic zone. There is a narrow band of chlorenchyma outside the sclerenchymatous ring; and between this and the epidermis is a discontinuous band of collenchyma several cells in width which is interrupted by the chlorenchyma at regular intervals. The epidermis is regular with a thin, smooth cuticle, and stomata occur, where it is subtended by chlorenchyma, in a frequency of about 20 per sq. mm. Numerous rigid multicellular hairs are produced on somewhat raised bases; and of the four types of hairs occurring in the Cucurbitaceae, three are present on the stems of *C. Pepo*. These are sharp-

pointed, conical hairs; short-stalked, and long-stalked, glandular ones.

The bundles are bicollateral but not as large as those in the hypocotyl, and there is less cambial activity. The size of the secondary xylem vessels is about the same as in the root, and the sieve tubes may be larger, reaching a diameter of 0.088 mm. There is frequently a well-defined inner cambium in the larger bundles which produces some phloem and parenchyma, but a lateral pericylary cambium is usually lacking. Isolated strands of phloem occur in the parenchymatous tissues of the pericyclic rays and medulla; and, to a limited degree, in the parenchyma between the epidermis and the sclerenchymatous ring. Commissural or connective sieve tubes serve to join all the phloem elements into a continuous system.

Crafts (4) has described the sieve tubes as being of two types: (1) the central tubes of the phloem proper which consist of short, broad elements; and (2) the peripheral tubes, including commissural, entocyclic, and ectocyclic phloem, which vary greatly in length, but tend to be of uniform diameter. Slime droplets occur in the young sieve tubes, and protoplasmic connections, which are continuous with the parietal cytoplasm, traverse the sieve plates connecting successive elements in mature sieve tubes. Callus develops around each cytoplasmic strand that passes through the sieve plate, and the callus cylinders increase in diameter until they fuse laterally to form a perforated plate which increases in thickness. The callus may become definitive, and slime plugs occur under certain conditions. In the peripheral phloem the appearance of the definitive callus takes place late in the ontogeny

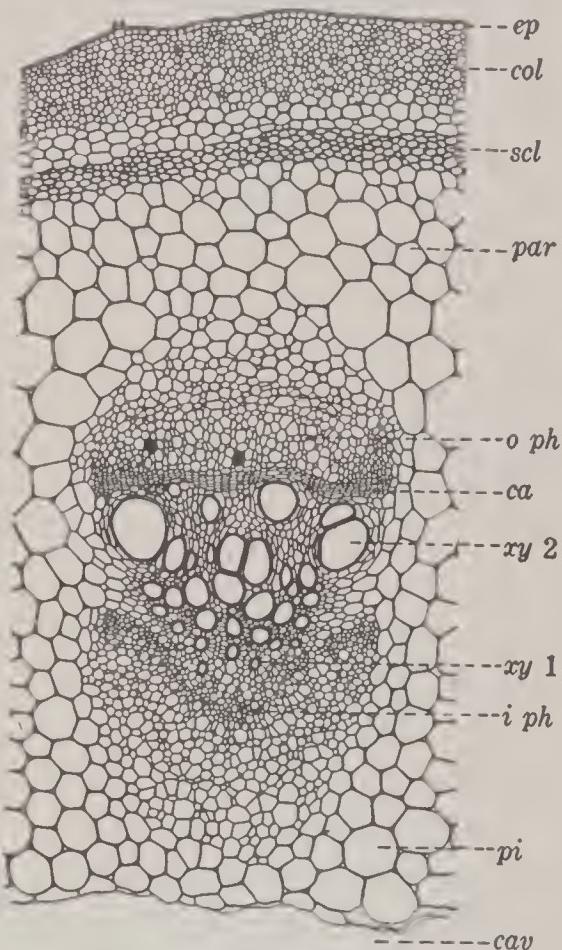


FIG. 321. Transection of sector of mature stem: *ca*, cambium; *cav*, medullary cavity; *col*, collenchyma; *ep*, epidermis; *i ph*, inner phloem; *o ph*, outer phloem; *par*, parenchyma; *pi*, pith; *scl*, sclerenchyma; *xy 1*, primary xylem; *xy 2*, secondary xylem.

of the sieve tube in conjunction with its obliteration or partial collapse.

On the basis of the structural characteristics of the sieve tubes, Crafts proposed that the movement of substances might take place "partly through sieve tube lumina and partly through phloem walls," but the subject of translocation is a controversial one and physiologists are by no means in agreement on this point. In this connection, the role of the phloem parenchyma in translocation has been generally ignored, and it seems very probable that a considerable proportion of the materials translocated in plants is moved through parenchymatous tissues.

THE LEAF. — The leaves are relatively thin as compared with other cucurbits. The radial walls of the upper epidermal cells are straight, while those of the lower epidermis are sinuous in outline. The stomatal frequency in *C. Pepo* is about 150 per sq. mm. for the upper surface as compared with about 350 on the lower one. Hairs are also more abundant on the lower surface than on the upper in a ratio of approximately four to one, there being about 80 per sq. mm. on the former. According to Yasuda (42), the lower epidermis in *C. Pepo* may be two or three layered in some places; and at these points, the leaf has an etiolated appearance. The palisade region comprises about three-fifths of the thickness of the blade, consisting in some parts of a double row of cells, and there are from two to six layers of loosely organized isodiametric parenchymatous cells in the spongy region.

The subterete petiole is slightly grooved on its adaxial surface and the center is hollow throughout. A limited number of stomata occurs in the epidermis, the frequency being approximately 12 per sq. mm.; and trichomes develop as in the blade. Strands of collenchyma occur outside the ring of fibrovascular bundles which are arranged in pairs, except for the largest one which extends along the abaxial side of the petiole.

THE TENDRIL. — As described by van Tieghem (37), the branched tendril of the cucurbits is a shoot, the terminal portion being a specialized leaf arising on a branch. This appears to be an axillary branch, but it is actually a terminal structure that is laterally displaced owing to the sympodial system of branching. Lisk (26) has pointed out that, although the physiology of the tendril has received exhaustive study, there has been relatively little work done on its anatomical structure. In *C. Pepo*, the proximal portion

of the tendril is subterete with a central hollow in its main unbranched section. In the intermediate portions, it is more or less polygonal, and the distal part is somewhat dorsiventrally flattened. (Fig. 322, A, B.) Haberlandt (14) observed that the tendrils are sensitive only on the abaxial side, which is usually devoid of hairs. There are a few stomata which occur in other sectors of the epidermis in a frequency of about 16 per sq. mm.

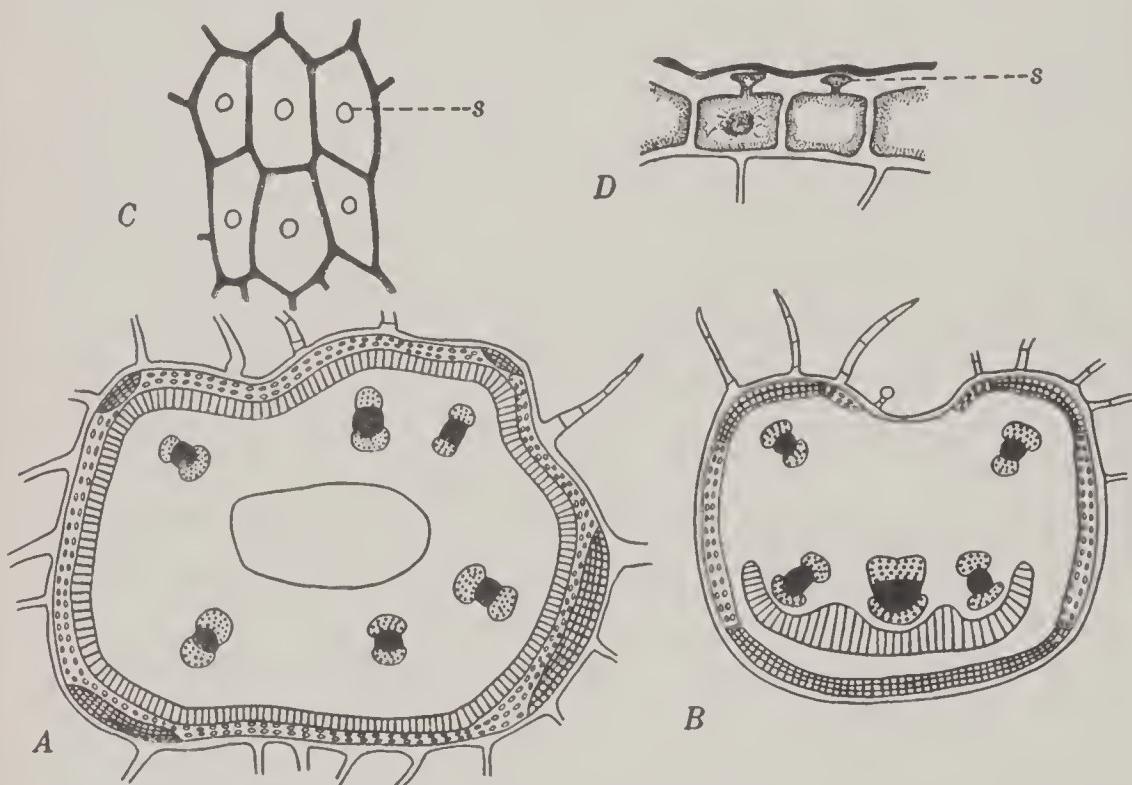


FIG. 322. A, diagrammatic transection of proximal portion of tendril showing distribution of vascular bundles and mechanical tissue; B, transection of distal portion in region of curvature. The diagrams are oriented with adaxial surface uppermost. The epidermal cells of abaxial surface contain sensory spots shown in C. These spots are underlain by tactile pits as shown in transection of similar cells in D. The pit (s) may contain a small crystal of calcium oxalate. In A and B, collenchyma is indicated by cross-hatching; sclerenchyma is lined; and chlorenchyma is designated with chloroplasts. The phloem of bicollateral bundles is stippled and xylem is black. (C and D, redrawn after Strasburger, *Textbook of Botany*.)

The epidermis of the sensitive portion of the tendril is unlike that of other regions in several respects. The cells are usually smaller and the outer walls have little cuticle until after the tendril is attached to a support, when they become thick and heavily cutinized. Haberlandt found that the sense epithelia on the sensitive side are located above a continuous wide band of collenchyma. The sense cells are somewhat stretched; and, in the center of each outer wall, there is a single sensitive spot or papilla. (Fig. 322, C.) The interior of the papilla forms a

funnel or tactile pit, and a canal leading from it enters the lumen of the cell which has a thick layer of cytoplasm containing chloroplasts and a large nucleus. (Fig. 322, D.) The papilla is completely filled with cytoplasm and a small crystal of calcium oxalate usually lies in it, although sometimes the crystal may be located in the canal leading to the cell. As in the cystoliths which occur in the epidermal hairs of *Cannabis*, the function of these crystals is not definitely known. They may be entirely non-functional excretion products, but it is possible that they are related to the irritability of the tactile cells.

Within the epidermis is a layer of collenchyma which is variously distributed in different parts of the tendril. In *C. maxima* and *C. Pepo*, Penhallow (32) found the collenchyma interrupted on the adaxial surface, and on the right and left flanks by chlorenchyma in which intercellular spaces subtend the stomata. Within the collenchyma, there are three or four rows of large parenchymatous cells. The sclerenchyma forms a continuous ring in the proximal portion of the tendril, but occurs only on the abaxial side in the distal part. At the base, the five to seven vascular bundles are arranged in a ring around the hollow central region.

Müller (29) found evidence of sclerenchyma in the tendrils of cucurbits in the bud stage, and observed a progressive lignification of this tissue and the xylem as the tendril matured. The portion of the tendril which surrounds a support becomes swollen, hard, and brittle owing to the enlargement and lignification of the cells of the epidermis, parenchyma, and collenchyma. In contrast, the portion which forms the spiral is not generally lignified except the xylem and sclerenchyma; and, as a result, this part remains more elastic.

Dastur and Kapadia (7), in investigating the mechanism of curvature in the tendrils of cucurbits, found that the parenchymatous cells on the convex (adaxial) side of the tendril elongate and produce the curvature, while the character of the mechanical tissue on the concave (abaxial) side tends to prevent elongation of this surface. The abaxial surface shows the effect of pressure resulting from curvature since the transverse walls are thrown into folds that project into the lumina of the cells. Actual measurements of the cells of the epidermis, and of the underlying rows of cells on the adaxial or convex side, indicate an average increase in length of 69.1 per cent.

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CHAPTER XX

COMPOSITAE

LACTUCA SATIVA

ALTHOUGH the composite family is one of the largest in the plant kingdom, it includes relatively few representatives of economic importance. Of those grown as vegetable crops, but two are outstanding: lettuce, *Lactuca sativa* L., and the globe artichoke, *Cynara Scolymus* L. Another member of this group is the Jerusalem artichoke, *Helianthus tuberosus* L.; and other less important ones include endive, *Cichorium endiva* L.; chicory, *C. intybus* L.; and salsify, *Tragopogon porrifolius* L. Of these forms, lettuce is by far the most important, ranking as one of the larger crops in Arizona and California.

The plant has enjoyed recent popularity and was also well regarded by the ancients. According to de Candolle (4), it has been in cultivation for more than 2000 years and is said to have been served on the tables of the Persian kings in 400 B.C. Because of its long usage, the relationship of the cultivated form to the numerous wild species is not definitely known. It is thought by most authorities that it may be a descendant from the compass plant, *Lactuca scariola* L., which was introduced into this country from Europe and now grows throughout the United States as a weed.

Bailey (1) recognizes four fairly distinct horticultural types: (1) *L. sativa*, var. *capitata*, Hort., which is the common cabbage type forming a head; (2) *L. sativa*, var. *intybacea*, Hort., or cut-leaved lettuce which is loosely spread; (3) *L. sativa*, var. *romana*, Hort., or Cos lettuce, whose leaves grow rapidly erect, forming a conically shaped plant; and (4) *L. sativa*, var. *augustana*, Hort., known as asparagus lettuce, with long entire leaves that have a slightly spreading habit. In commercial practice, the nomenclature has become extremely confusing owing to the large number of trade names that have been given to the numerous variants

of the four principal types. This is illustrated by Morse (18), who has compiled a list of approximately 1100 names that have been applied to the lettuce varieties in this country. This involves tremendous duplication as there are probably less than 150 distinct varieties even on the basis of minor differences. In order to clarify the situation, Morse has described the forms which he regards as constituting the standard American varieties. Twenty-two types are included, the most important being the New York variety which, with its sub-type Imperial, is estimated to represent approximately half of the commercial lettuce crop grown for shipment.

GENERAL MORPHOLOGY

The lettuce plant is an annual; and, as the generic name implies, one of its important characteristics is the presence of a milky juice or latex. In head lettuce, the plant may produce heads in 65 to 90 days depending upon the strain used; while in California, where a majority of the seed is grown, the crop is planted in late December or January and the fruits begin to ripen early in August. (Fig. 323.)

THE ROOT. — The plant has a strong fleshy tap root which develops very rapidly. Weaver and Bruner (29) have described the development of the root system and find that under favorable conditions the tap root may elongate at the rate of an inch per day, and, in some soils, may attain a maximum depth of over 6 feet by the time that the flower stalks are producing blossoms. The average depth is approximately 5 feet at maturity, and the major portion of the entire system occupies the first 2 feet of soil. The principal lateral roots arise in two rows chiefly in the first 10 inches of soil, extending outward for 6 to 18 inches and then downward. There are few laterals originating below the first foot of soil and many of the lower ones are short and thread-like. Those which arise from the upper portion of the tap root may equal it in length, and like it attain a diameter of an inch or more.

THE SHOOT. — At first, the plant develops a fleshy crown stem from which basal leaves arise in an alternate spiral phyllotaxy, the degree of compactness varying with the variety. (Fig. 324.) In some instances, they form such a firm, solid head that in the production of seed it must be partially cut open in the field in

order to permit elongation and emergence of the seed stalk. In the non-heading types, the basal leaves are less compact and more spreading; while, in the Cos or Romaine types, they are semi-erect

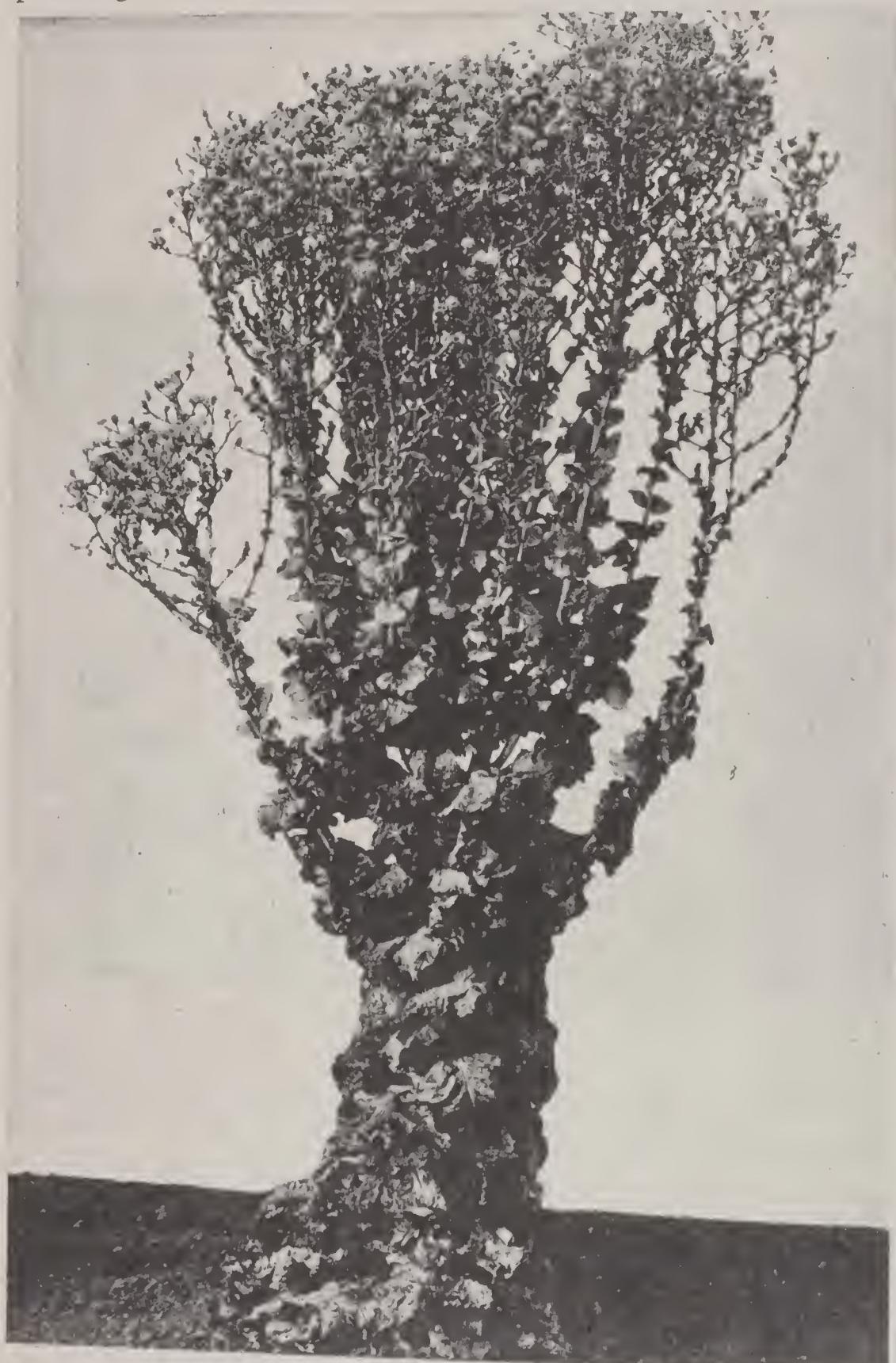


FIG. 323. Lettuce plant in seed. (Courtesy of the Ferry Morse Seed Co.)

to erect. The leaves vary in color from light to dark green; and, in some forms, this is modified by a reddish or brown pigment. This accessory pigment may be light, medium, or dark in intensity and is a sufficiently constant character to be used in the descriptions of commercial varieties.

Cabbage varieties, known as butter heads, are so called because of their flavor and the oily appearance of the inner leaves, which



FIG. 324. Field of lettuce in head, variety New York. (Courtesy of the Ferry Morse Seed Co.)

are thick and soft in texture with entire margins. The leaves of the crisp or curled cabbage types are brittle with conspicuous veins and margins that are crinkled or curled. Non-heading or bunching varieties may have leaves of either the butter or the crisp type. In cut-leaved lettuce, the loosely spreading leaves are 6 to 10 inches long and deeply incised on the edges. The Cos variety has spatulate leaves that are long and entire or sometimes sparingly dentate. They are upright in habit of growth and form

heads 1 or 2 feet in height. In the asparagus type, the lanceolate leaves are 6 to 12 inches in length, 1 or 2 inches in width, usually entire but sometimes lobed.

THE INFLORESCENCE AND FLOWER. — The floral axes reach a height of 2 to 4 feet or more and form a branched, bushy crown. The branches bear leaves that are commonly sagittate and clasping and are terminated by the inflorescences. The inflorescence consists of a cymose cluster of heads each of which contains from 15 to 25 or more flowers, although fewer may occur in some instances. The oldest head of the inflorescence is the terminal one, and the lateral heads are axillary. (Fig. 325, A.) The ligulate flowers are all perfect and alike. The flower primordia arise simultaneously from a naked receptacle which is at first conical, then convex, and finally flat and broad. (Fig. 326, A.) As the individual primordium enlarges, a marginal ring forms, which marks the initiation of the corolla tube. (Fig. 326, B.) This elongates and a fold of meristematic tissue arises at the base of its adaxial surface from which the staminal ring develops. At the same time, a ring of tissue is formed outside and at the base of the corolla tube which gives rise to the pappus. (Fig. 326, C, D.) The carpillary primordia are the last to appear; and, by the time they begin to differentiate, the corolla has started to incurve over the tip of the floral axis. (Fig. 326, D, E.) The single cavity of the ovary is formed by the upward growth of the carpillary tissue. The growth of the undiverged tissue of the carpels, corolla tube, and calyx tube results in the elevation of the anthers, the strap of the

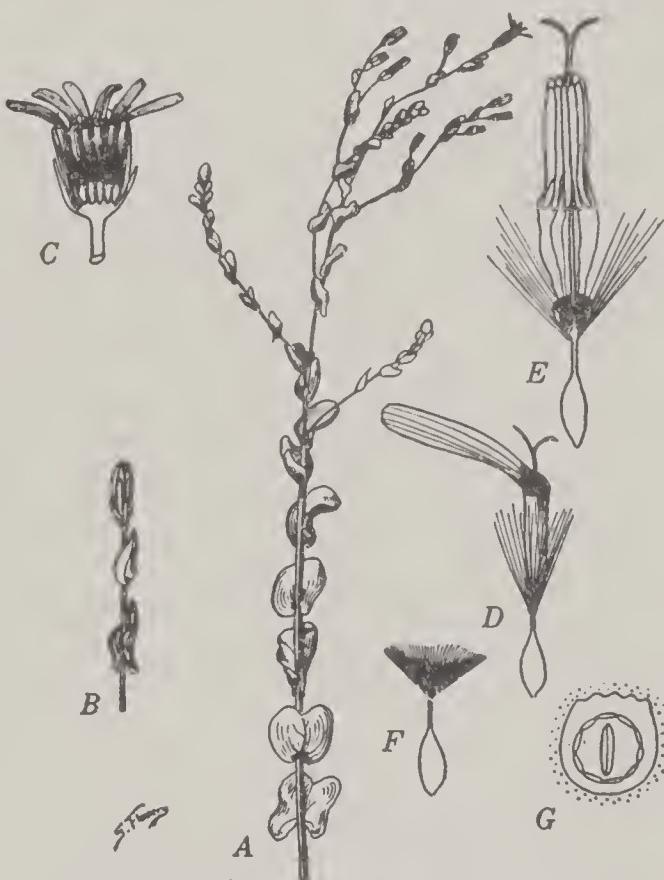


FIG. 325. A, habit of flower; B, unopened head; C, longisection through head; D, single flower; E, flower with corolla removed; F, akene with pappus; G, floral diagram.

ligulate corolla, and the pappus so that the flower is epigynous. (Fig. 326, E, F.)

The mature pappus is white, fine, and soft, and ultimately functions in the dissemination of the fruit. (Fig. 325, D, F.) The sympetalous ligulate corolla is yellow or whitish yellow, and the truncate, five-toothed ray consists of five undiverged petals. Each ray inclines obliquely outward so that the expanded head is about a centimeter and a half in diameter. (Fig. 325, C, D.) The

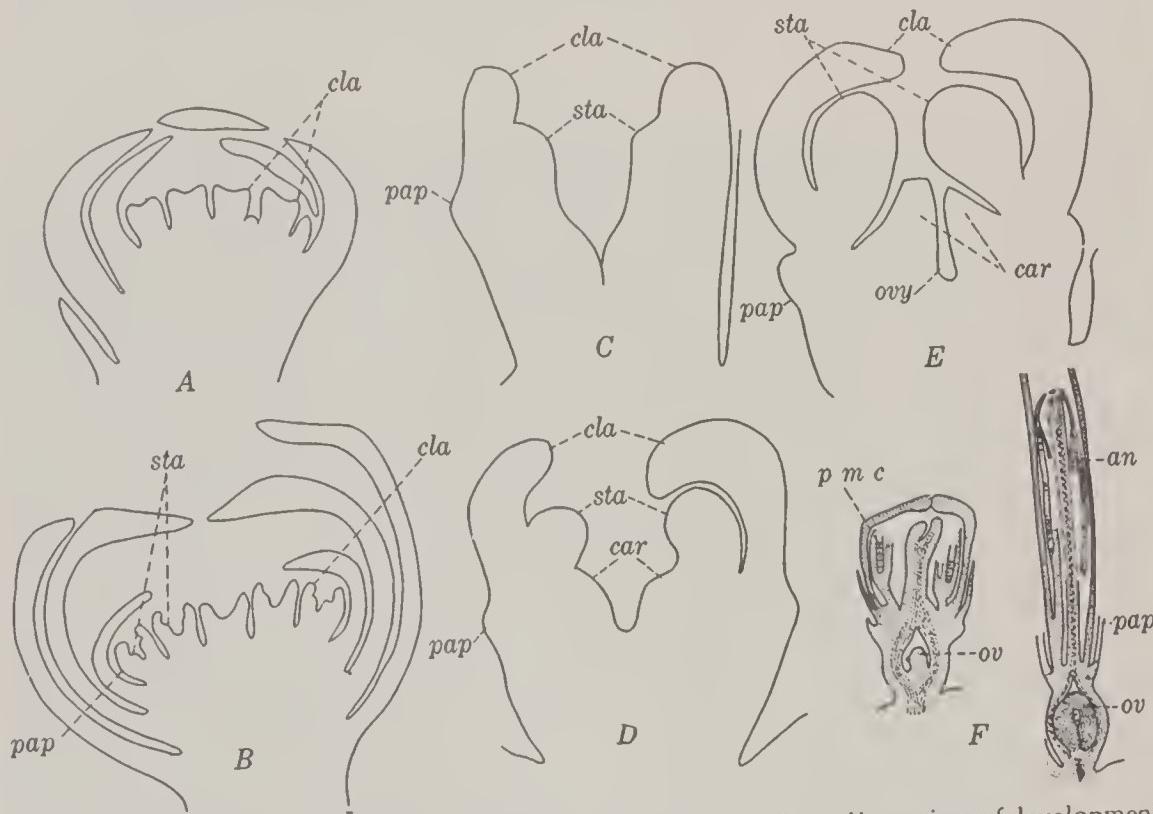


FIG. 326. Floral development: A, head, showing flower primordia at time of development of corolla; B, same, showing development of corolla, stamens, and pappus; C, D, and E, successive stages in development of individual flower; F, longisection through flower showing early and later stages in development; an, anther; car, carpel; cla, corolla; ov, ovule; ovy, ovarian cavity; pap, pappus; pmc, pollen mother cells; sta, stamens. (After Jones, *Hilgardia*.)

filaments of the five stamens are diverged from the base of the corolla tube as separate structures, but the anthers are united, forming a cylinder which projects beyond the corolla tube and surrounds the style. The ovary is unilocular and the slender style is unbranched up to its point of emergence from the anther cylinder where the two stylar branches terminate in a two-lobed stigma. (Fig. 325, D, E.) The head is surrounded by a cylindrical involucre consisting of a series of bracts that are closely imbricated in the bud, the outermost bracts being shorter than the inner ones. (Fig. 325, B.)

MEGASPOROGENESIS. — In most cases, a single ovule arises at the base of the ovary, but the occurrence of two or more ovules is not uncommon. There is an early differentiation of a single hypodermal archesporial cell which, according to Jones (13), functions as a megaspore mother cell. (Fig. 327, A.) The nucellar tissue consists of a single layer; and it never becomes thicker, since its cells divide only anteclinally as the megaspore mother cell enlarges. The one massive integument begins to differentiate at about the time the megaspore mother cell is clearly differentiated, and its unilateral growth results in a gradual curvature of the ovule until it becomes completely anatropous. (Fig. 327, B, C.) This is accomplished by the time the first or heterotypic division of the megaspore mother nucleus occurs.

The formation of the linear tetrad of megasporangia is similar to that reported for related genera. The three micropylar megasporangia disintegrate and the innermost one is functional forming an eight-nucleate megagametophyte by successive nuclear divisions. Jones did not observe an early fusion of the polar nuclei as is reported for some composites, and states that it occurs at the time of fertilization. Although the number of antipodal cells has been reported as variable for other members of this family, he was unable to observe more than three in any instance. This seems to be the constant number for most of the investigated Cichorioideae. A conspicuous integumentary layer, which persists until the seed is almost mature, surrounds the megagametophyte and is regarded as having a nutritive relation to the developing embryo.

MICROSPOROGENESIS. — Microsporogenesis is initiated by the development of a single row of hypodermal archesporial cells. These divide periclinally to form a row of pollen mother cells and

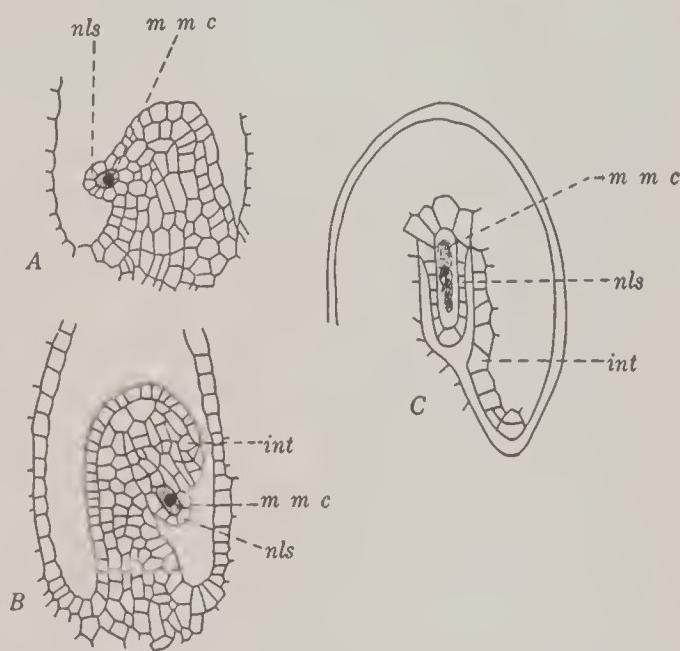


FIG. 327. A-C, stages in development of ovule: *int*, integument; *m m c*, megaspore mother cell; *nls*, single-layered nucellus. (After Jones, *Hilgardia*.)

an outer layer of cells, the latter by subsequent divisions forming the tapetum, the middle layer, and the endothecium. Gates and Rees (10) report that there are from 15 to 20 pollen mother cells producing a total of about 60 pollen grains. They observed that the pollen mother cells frequently separate before synapsis and this is confirmed by Jones. The walls of the microspores are formed by furrowing which is initiated at the periphery of the mother cell and extends centripetally until the four furrows meet. Following the secretion of the walls of the microspores, the original wall of the mother cell disintegrates, and at about this time the tapetal cells become binucleate and later quadrinucleate. The nuclei may be more or less completely disintegrated even prior to the disorganization of the tapetal walls and finally a plasmodium is formed. The microspores continue their development within the anther and undergo nuclear division so that at anthesis each pollen grain possesses a vegetative nucleus and two slender filamentous microgametes.

POLLINATION. — The floral buds elongate very rapidly in the 24 hours preceding anthesis, and the involucral bracts enclosing the head begin to open at the summit because of the development of the individual flowers within. The flowers open early in the morning and remain so for about two hours, after which the corolla closes tightly and does not again open. All the flowers of a single head open at one time; and, two or three days later, the corollas, stamens, and the wilted styles and stigmas are shed. In California, where a large proportion of the lettuce for seed purposes is grown, the crop is usually ready for harvest in July or early August; but, in some places, the flowering peak may occur in June and individual plants may produce flowers over a period of two months or more.

The mechanism of pollination which has been described by Knuth (15), Jones (13), Oliver (19), and Thompson (27) is such that the flowers are almost entirely self-pollinated. Natural cross-pollination has been observed, however; and, on the basis of genetic experiments, Thompson found that natural crossing occurred in 20 different populations in percentages ranging from 1.33 to 6.22, indicating that "the extent of natural crossing may be greater than is generally believed." Insect visitations have been observed in several instances, which also suggests that there is opportunity for cross-pollination.

The method of pollination is related to the structure and ontogeny of the flower. The stigma develops papillae on its inner surface and these become hairs by the time the stigmatic lobes expand. On the outer surfaces of the stigmas and style, brush hairs are developed; and, since the anthers dehisce before the flower head opens, these hairs gather masses of pollen as they are pushed through the anther cylinder by the elongation of the style. Knuth has stated that following the emergence of the stigmas, "they ultimately roll back into a complete circle, so that automatic self-pollination necessarily results from contact of the stigmatic papillae with the pollen-grains clinging to the sweeping-hairs." Jones found that, in some varieties at least, the backward revolution of the stigmatic lobes was not as complete as reported by Knuth. There were a few pollen grains on the inner stigmatic surface, but the edges of the stigmatic lobes were always covered with pollen as well as the backs and he pointed out that "it is not known definitely whether or not the pollen grains will germinate elsewhere on the pistil than on the stigmatic papillae."

FERTILIZATION AND EMBRYOGENY. — Fertilization follows soon after pollination, and at the end of six hours, there may be some two-celled embryos, while in practically all flowers fertilization is completed. In double fertilization the second microgamete and the two polar nuclei unite almost simultaneously to form the endosperm nucleus.

Jones (13) has investigated the embryogeny in *Lactuca* and finds that it agrees in general type with that of other Compositae as reported by Carano (5) and Souèges (26). Following fertilization, the zygote elongates and develops a definite cell wall; and, shortly thereafter, the first division of the zygote occurs. This is transverse and cuts the zygote into a terminal cell, *a*, from which the cotyledons and epicotyl develop, and a lower cell, *b*, which forms the hypocotyl. (Fig. 328, *A*.) In the formation of the four-celled embryo, the cell *a* forms two cells by a longitudinal division, while cell *b* divides transversely to form two daughter cells, *c* and *d*. (Fig. 328, *B*.)

In the formation of the eight-celled embryo, the initiation of nuclear activity seems to be apical, and each tier of cells usually divides slightly in advance of the cells below it. In the eight-celled stage, tier *a* has four cells, tier *c* two cells, and *e* and *f* are derived from the division of cell *d*. (Fig. 328, *C*.) The 16-celled

stage is reached about 25 hours after pollination; and, as in the development of the latter, the cells of tier *a* are the first to divide so that an octant is formed and the embryo is temporarily in a 12-celled stage. No further divisions occur in tier *a* until all the lower tiers have undergone division. This occurs in sequence, tier *c* dividing first, followed by tier *e*, and the transverse division of cell *f* to form the daughter cells, *g* and *h*, thus completing the formation of the 16-celled embryo. (Fig. 328, *D*.)

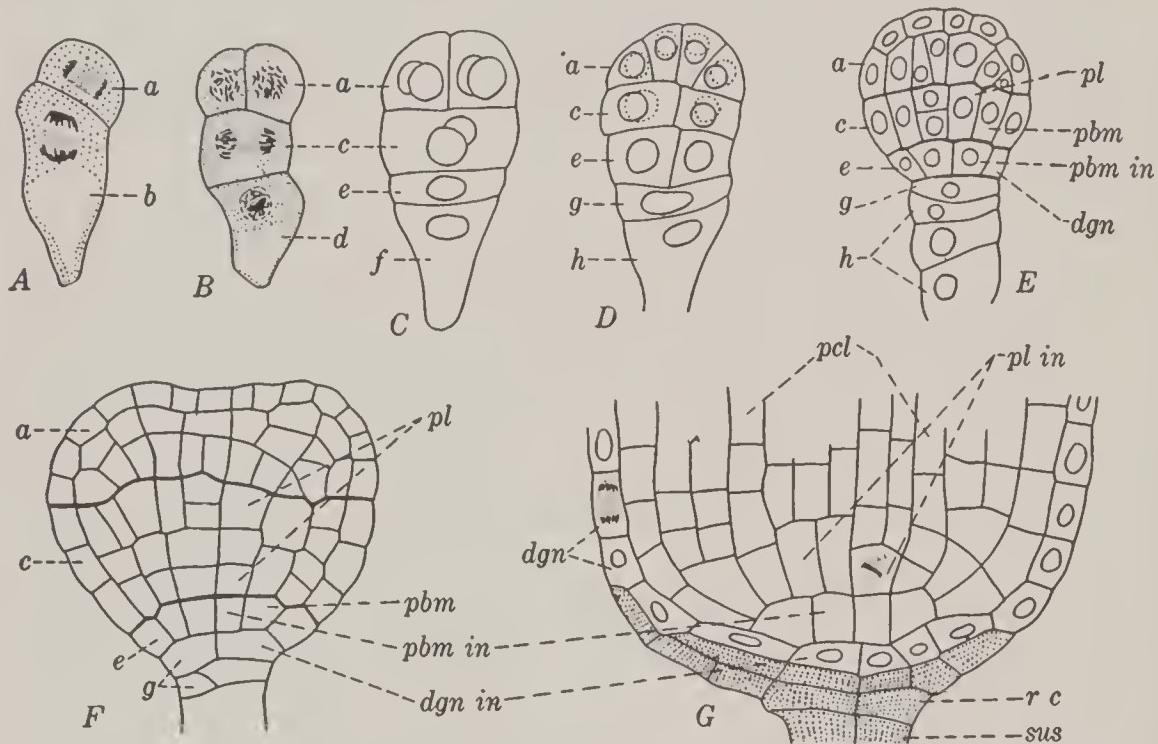


FIG. 328. Stages in embryogeny: *A*, two-celled embryo in process of division, 9 hours after pollination; *B*, four-celled embryo at 12 hours; *C*, eight-celled embryo at 20 hours; *D*, sixteen-celled embryo at 26 hours; *E*, embryo showing differentiation of histogens at 46 hours; *F*, initial lobing preceding formation of cotyledons at 3 days; *G*, lower portion of embryo showing differentiation of primary root. Letters *a* to *h* refer to the succession of cell divisions (description in text): *dgn*, dermatogen; *dgn in*, dermatogen initial; *pbm*, periblem; *pbm in*, periblem initial; *pcl*, pericycle; *pl*, plerome; *pl in*, plerome initial; *r c*, cells of root cap (this includes all shaded cells except those of suspensor, *sus*). (After Jones, *Hilgardia*.)

Beyond the 16-celled stage, it is difficult to follow the sequence of cell divisions; but the next development is the cutting off of definite histogens (dermatogen, periblem, and plerome) by the formation of tangential and vertical walls. (Fig. 328, *E*.) Three days after anthesis, slight elevations can be observed in tier *a* which later become the cotyledons. (Fig. 328, *F*.) Cell *g* undergoes transverse and longitudinal division to form two layers of cells, and those of the upper layer constitute the dermatogen initials while the lower ones contribute to the root cap. The derivatives

of cell *b* produce the suspensor, which is variable in length and in the number of its cells. (Fig. 328, *G*.)

ENDOSPERM FORMATION. — The divisions of the primary endosperm nucleus and the nuclei subsequently derived from it occur slightly prior to those of the embryo; and by the time the latter is four-celled, there usually have been four successive divisions of the endosperm nuclei. About 20 hours after pollination when the embryo is eight-celled, wall formation is initiated in the endosperm; and its cells completely fill the embryo sac. They continue rapid growth and division, keeping pace with the enlarging cavity; but the developing embryo grows more rapidly than the endosperm which it digests, and a week after pollination the endosperm is almost entirely resorbed. When the seed is mature, only the two outermost layers of endosperm remain. These are closely appressed to the cell walls of the innermost layer of the integument, forming a membrane which completely surrounds the embryo.

ANATOMY

FRUIT AND SEED. — During the preceding developments which take place within the young akene, the bracts of the involucre are tightly compressed about the developing fruits. The beak of each fruit elongates and rapidly lifts the pappus upward, so that within four or five days after anthesis it appears through the bracts. In the New York variety, Jones found that approximately 12 days elapsed from anthesis to fruit maturity, subject to variation due to temperature and other factors. In this variety, the heads contain about 18 flowers and produce a slightly smaller number of normal akenes.

The beaked akene is spindle- or lance-shaped with a surface that has a number of longitudinal ribs. Kondo (14) found a variation of from 13 to 23 in 22 varieties. In the New York variety, the average length of the akene is 4.2 mm.; the breadth 1.1 mm. and thickness 0.4 mm. Cummings (8) has determined that size of seed is a factor in production, stating that

"the merits of large seed in lettuce culture were shown in the production of larger seedlings, an increased weight of edibly matured plants, which displayed better heading-up capabilities, earliness and uniformity in filling the heads; in short, augmented earliness and quality."

Borthwick and Robbins (3) have investigated the anatomy of the fruit and seed coat. In the young ovary, just prior to anthesis, the nucellar tissue surrounding the megagametophyte is almost entirely digested, and the massive integument of the single anatropous ovule consists of from 12 to 18 rows of parenchymatous cells. The innermost layer is readily distinguishable from the others because of the larger size of its cells. Even at this early stage,

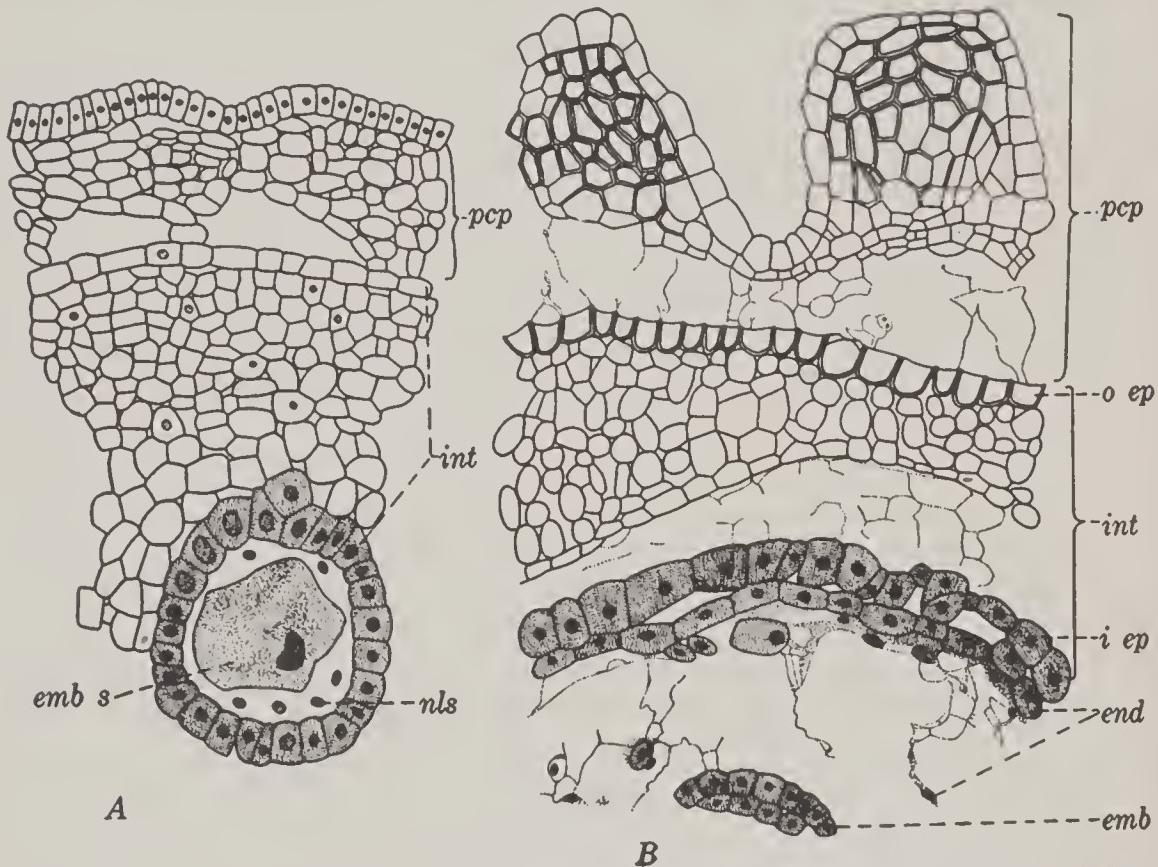


FIG. 329. A, transection of portion of ovary 2 hours after anthesis; B, transection of akene 7 days after anthesis: *emb*, embryo; *emb s*, embryo sac; *end*, endosperm in which some wall formation is still in progress; *i ep*, inner epidermis of integument; *int*, integument; *nls*, disintegrating cell of nucellus; *o ep*, outer epidermis of integument; *pcp*, pericarp. (Redrawn after Borthwick and Robbins, *Hilgardia*.)

the integumentary parenchyma may give evidence of some disintegration. The pericarp varies in thickness and its cells resemble those of the integument except that they are somewhat smaller. There is a distinct outer epidermis; but, by the time anthesis occurs, lysigenous cavities have begun to develop in the inner portion of the pericarp, and disintegration of all except the outermost layers of the ovary wall proceeds rapidly. (Fig. 329, A.) A week after anthesis, there is further disintegration of the tissues of pericarp and integument as the embryo enlarges and the endosperm is formed. By the tenth day, the cells of the inner epidermis

of the integument are disorganized, and the inner walls of the laterally placed epidermal cells may invest the endosperm so closely that they appear to be a part of it. Borthwick and Robbins determined that this translucent integumentary membrane is continuous and semi-permeable.

As the akene matures, the ribs of the pericarp develop. (Fig. 330, A, B.) These are rather equally spaced and consist of thick-walled sclerenchymatous fibers which are pitted and lignified.

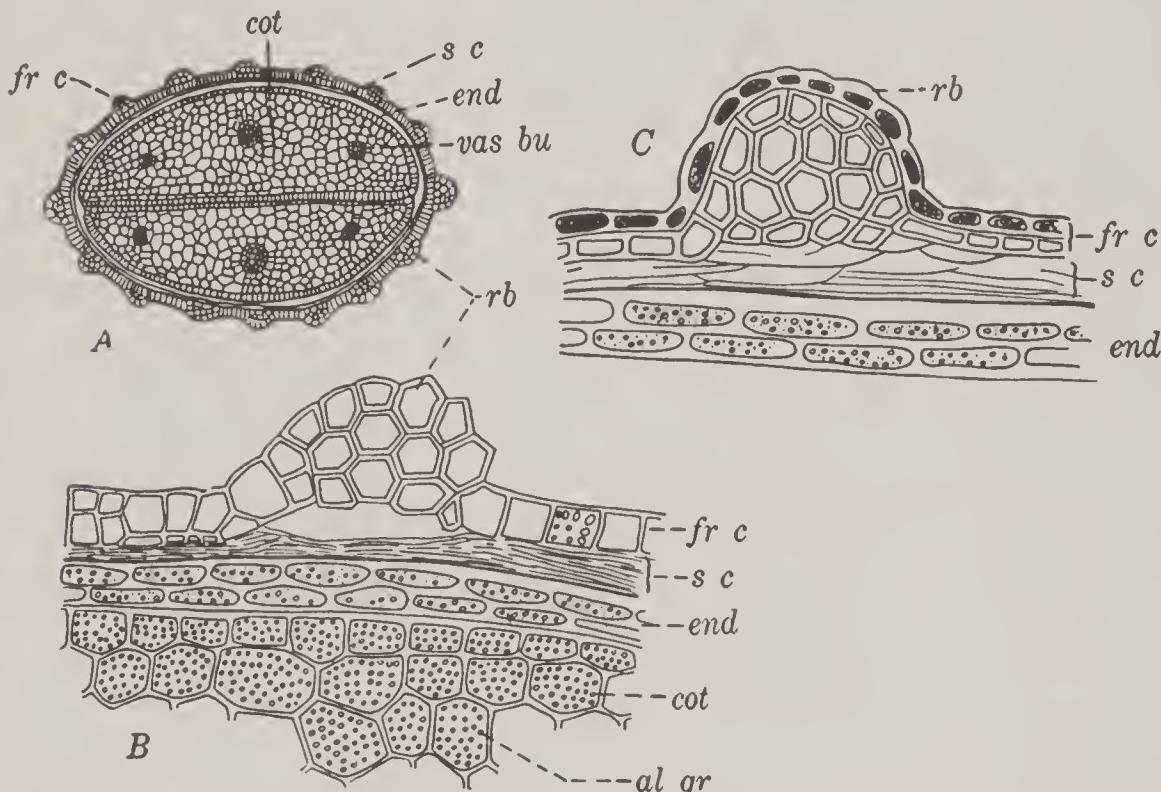


FIG. 330. A, transection of akene; B, transection of portion of fruit coat of light-colored akene; C, same of dark fruit: *al gr*, aleurone grain; *cot*, cotyledon; *end*, endosperm; *fr c*, fruit coat; *rb*, rib; *sc*, seed coat; *vas bu*, vascular bundle. (Redrawn after Kondo, Ohara Institute.)

The remainder of the pericarp in the mature akene is only one or two cells in thickness since the other cells of the parenchymatous portion of the fruit coat become disorganized. There is a wide range in the color of the fruit from buff to dark brown and from light gray to carbon gray or black. This difference is due in part to the presence or absence of pigment in the epidermis of the pericarp. In the dark-colored fruits, the outer epidermis is filled with a dark brown pigment which is entirely lacking in the light-colored fruits. (Fig. 330, B, C.)

The cells of the mature integument are much crushed and partially disintegrated, but the outer epidermis may persist as a

thick-walled layer. The suberized semi-permeable membrane referred to above, which is a part of the wall of the inner epidermis, lies adjacent to the endosperm. In most parts of the seed, the endosperm is two cell layers in width; but, adjacent to the tip of the primary root, it may be three or four cells in thickness. Its cells are thick-walled; and, in some cases, projections from the walls extend into the cell cavities which are filled with fatty substances and protein granules.

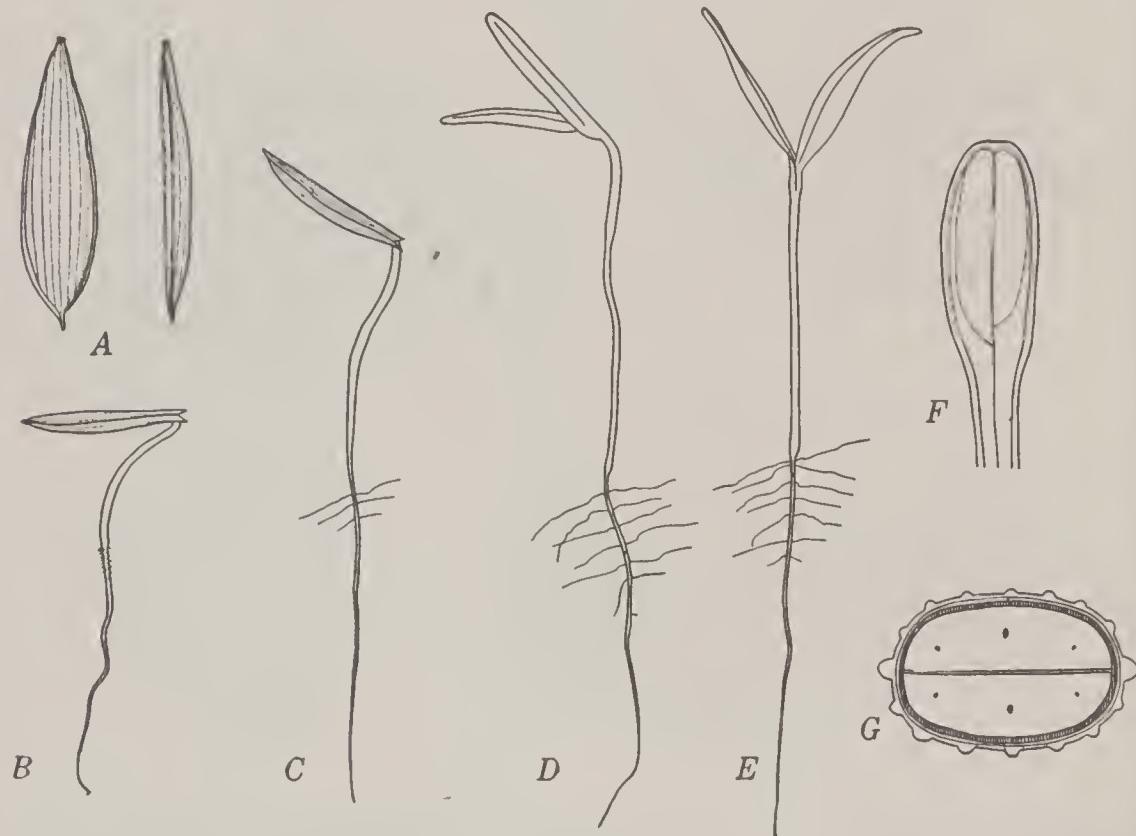


FIG. 331. *A*, surface and side views of akene; *B-E*, stages in development of seedling; *F*, outline of cotyledon showing pattern of main veins; *G*, transection through akene showing two cotyledons surrounded by endosperm, seed, and fruit coats, variety New York Regular.

DEVELOPMENT OF THE SEEDLING. — The optimum germination of lettuce seed is obtained where there is an adequate supply of water, a temperature not in excess of 25° C., and good aeration. Borthwick and Robbins secured the best results when the seed was stored in moist folds of burlap at 4° C. for a period of four to six days preceding planting. The percentage of germination falls rapidly at temperatures above 25° C. and may be completely inhibited at 30° C. in most varieties. The experimental evidence indicates that this inhibition is due to the structures surrounding the embryo, which consist of the two-layered endosperm and the semi-permeable membrane of the integument. These are thought

to retard gas exchange; since, when all of the pericarp, seed coat, and endosperm are removed from seeds, the naked embryos initiate growth within 24 hours. In cases where only the pericarp and

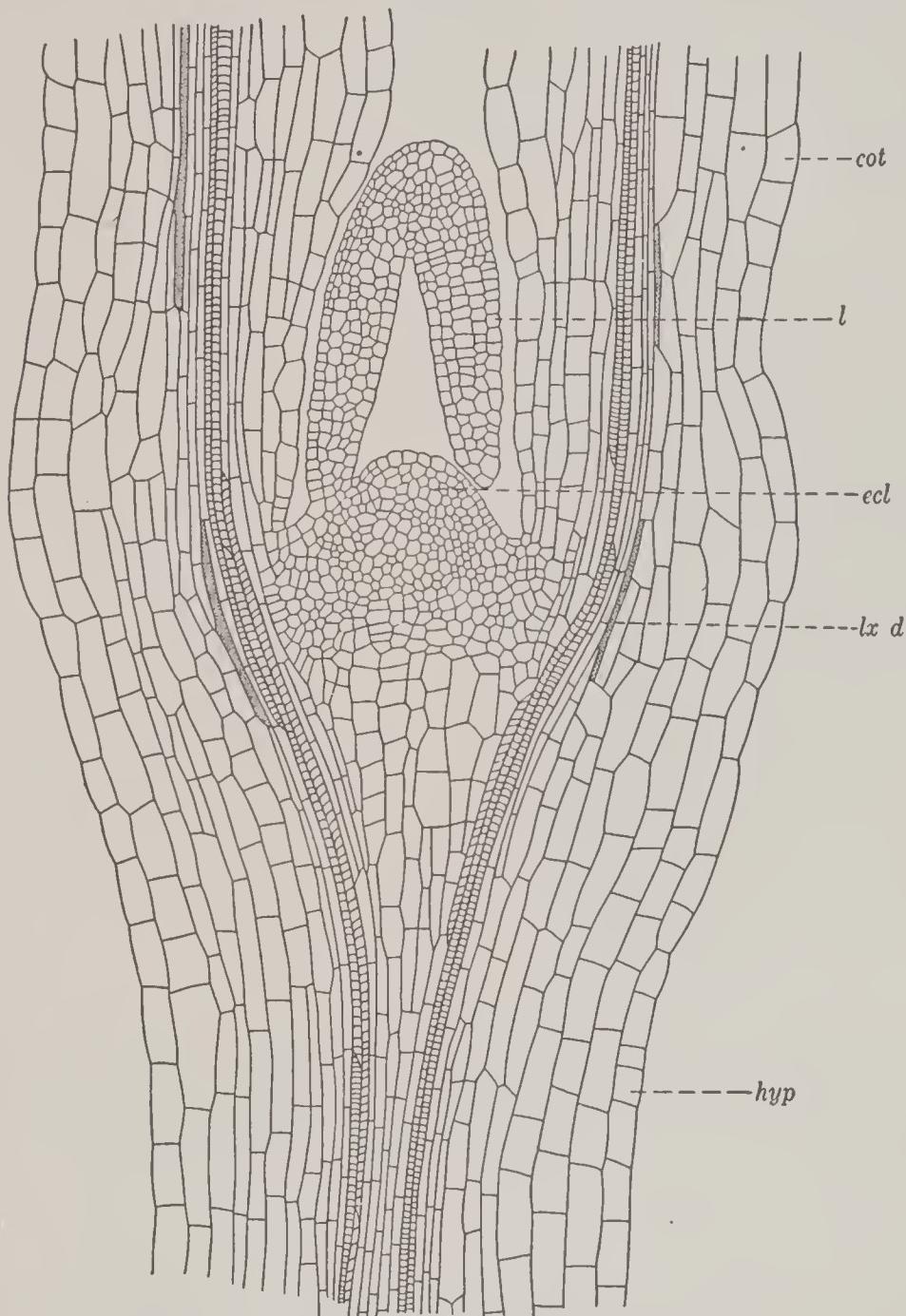


FIG. 332. Longisection through epicotyl and cotyledonary node of six-day seedling showing development of first foliage leaf and presence of lactiferous ducts. Cortical lactiferous ducts which occur in seedling axis are not shown in this plane, variety New York Regular: *cot*, cotyledon; *ecl*, growing point of epicotyl; *hyp*, hypocotyl; *l*, first foliage leaf; *lx d*,

outer portions of the seed coat were removed, so that the embryo remained enclosed by the endosperm and the integumentary membrane, Borthwick and Robbins found no germination at 30°C .

The tip of the primary root emerges from the basal end of the fruit coat and grows rapidly downward through the soil. This is followed by an elongation of the hypocotyl which raises the cotyledons and the partially enveloping remains of the akene. In some instances, the cotyledons are freed from the combined fruit and seed coats as they emerge from the soil. At the time of

emergence, the cotyledons are in a horizontal position; but as growth proceeds, they are reoriented until they are nearly vertical. (Fig. 331.) As the two blades expand laterally, the minute epicotyl is exposed; and, within a few days, the first foliage leaf appears. (Fig. 332.) The formation of lateral roots is initiated early; and in about six days, secondary roots appear on the first inch and a half of the primary root. They are usually diverged in two opposite double rows owing to the fact that they originate at a slight angle to and on each side of the two protoxylem points.

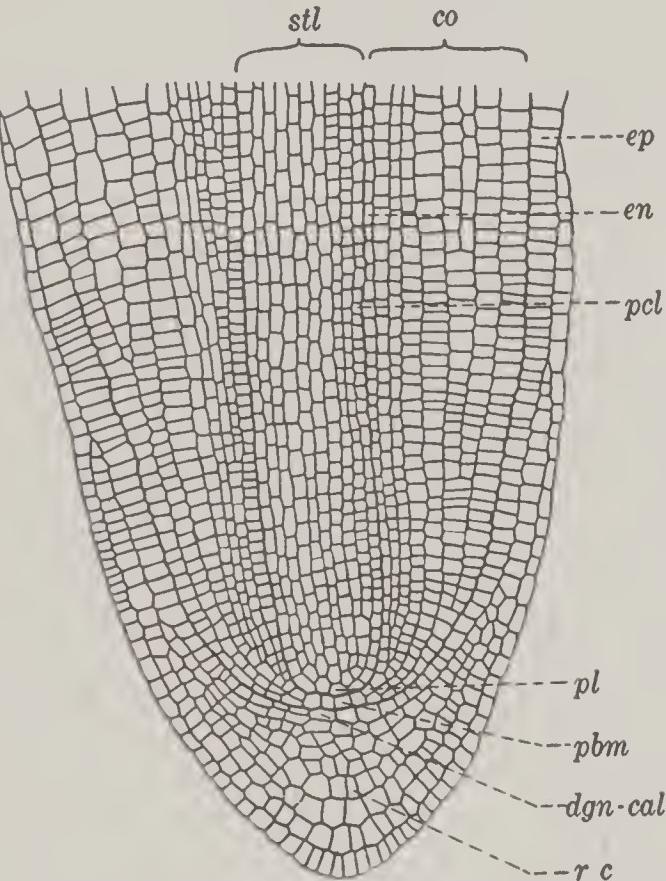


FIG. 333. Median longisection of tip of primary root showing histogens: *co*, cortex; *dgn-cal*, dermatogen-calyptrogen; *en*, endodermis; *ep*, epidermis; *pbm*, periblem; *pcl*, pericycle; *pl*, plerome; *rc*, root cap; *stl*, stele.

ONTOGENY OF THE PRIMARY ROOT. — The development of the primary root and the vascular anatomy of the seedling axis have been investigated by Port (22), who used the New York variety. The ontogeny of the root is similar to Janczewski's (11) third type, in which three histogens are differentiated that produce the stele, cortex, epidermis, and root cap. (Fig. 333.) As noted earlier, the histogens originate in the embryo and are well defined four days after pollination of the flower. (Fig. 328, *E*, *F*, *G*.)

The innermost histogen or plerome gives rise to a cylindrical stele. The cells of this region divide in all three planes, but

divisions in vertical planes predominate in connection with the differentiation of the vascular elements. This, coupled with axial elongation, results in the development of slender, much-elongated cells. The outermost layer of the plerome forms the pericycle, which can be distinguished early by the larger size of its cells. Centrad to the pericycle, activity can be observed at two opposite poles where the cells of the primary phloem are

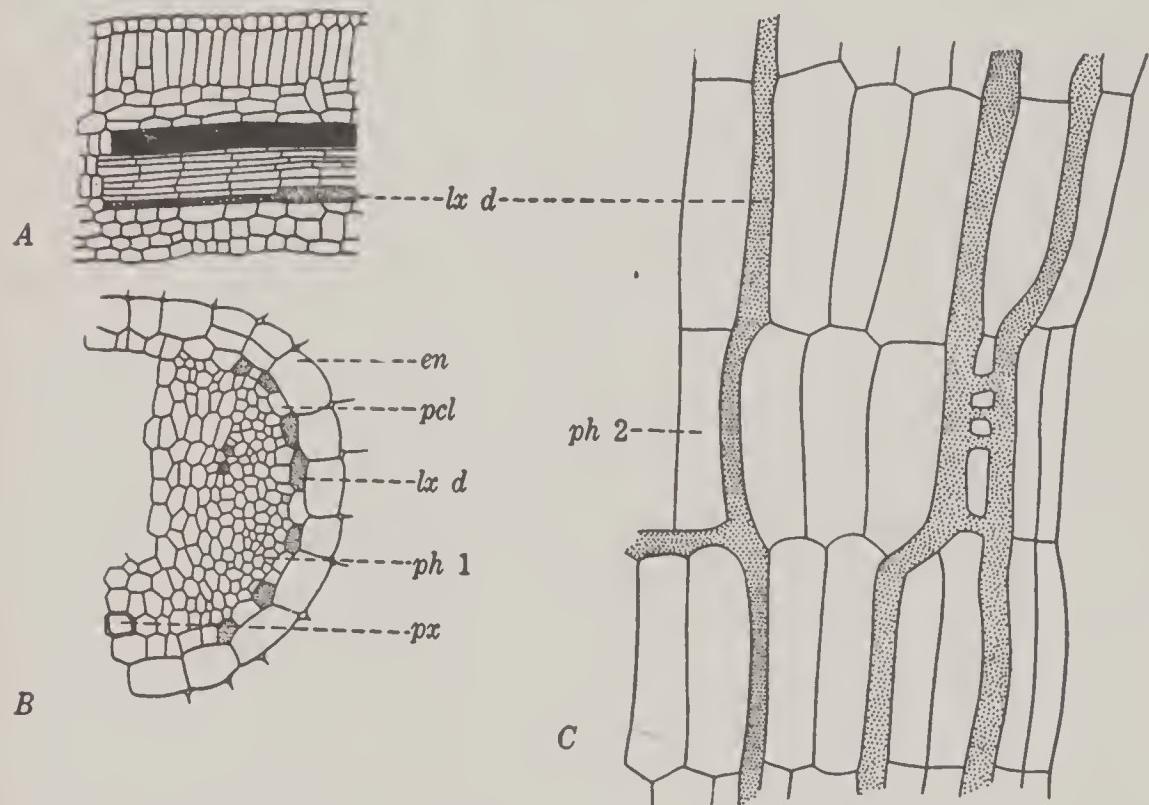


FIG. 334. Lactiferous ducts: A, longisection through cotyledon showing lactiferous duct on abaxial face of phloem; B, transection of portion of stele and endodermis of primary root of one-day-old seedling in which primary phloem and lactiferous ducts are formed and protoxylem has just begun to differentiate; tangential divisions of endodermis are shown; C, longisection through secondary phloem of old root showing lactiferous ducts with branches and cross-anastomoses, variety New York: en, endodermis; lx d, lactiferous duct; pcl, pericycle; ph 1, primary phloem; ph 2, secondary phloem; px, protoxylem.

formed. This occurs slightly in advance of the differentiation of the primary xylem, which is initiated on radii at right angles to the phloem. Abutting the pericycle, annular and spiral protoxylem vessels develop, establishing the two points of the diarch xylem strand. The maturation of the primary xylem elements progresses centripetally, and the last ones to be differentiated are the reticulate vessels that occupy the center of the axis and complete the primary strand. (Fig. 335.) Port has noted the occurrence of lactiferous ducts in the pericycle and primary phloem. These

are articulate and develop from a linear series of cells through the dissolution of the end walls. They are located in the arcs of the pericycle which lie outside the two groups of primary phloem, and additional ducts may also be differentiated on the centrad surface of the phloem. There are no ducts in the pericycle outside the protoxylem. (Fig. 334, B.)

The cortical cells are derived from the periblem. The endodermal layer adjacent to the pericycle consists of regularly arranged

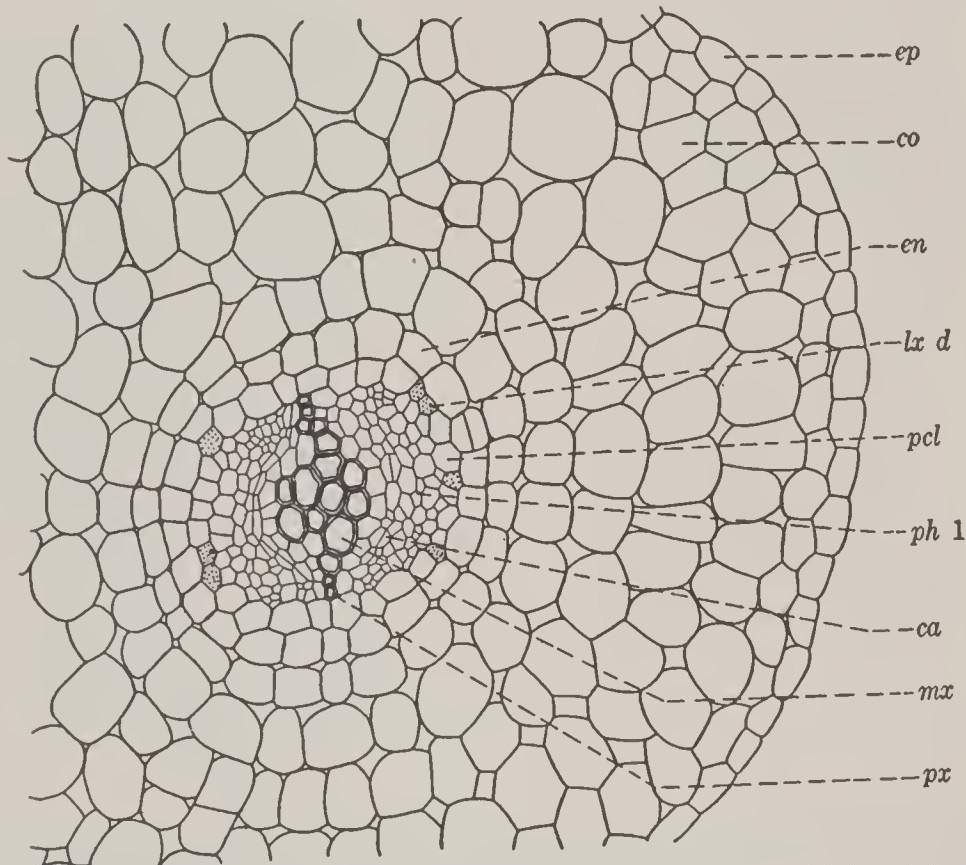


FIG. 335. Transection of portion of primary root at initiation of cambial activity showing lactiferous ducts in pericycle and tangential division of an endodermal cell, variety New York Regular: *ca*, cambium; *co*, cortex; *en*, endodermis; *ep*, epidermis; *lx d*, lactiferous duct; *mx*, metaxylem; *pcl*, pericycle; *ph 1*, primary phloem; *px*, protoxylem.

cells, and the differentiation of Caspary strips occurs at about the time that secondary thickening of the root is initiated. A unique development in the ontogeny of the endodermis is the tangential division of single cells or sectors of cells. This happens first in arcs lying outside the primary phloem, and finally the entire endodermis may become biserrate. Phillips (21) has described a somewhat similar situation for *Cynara*, also a member of the tribe Cichorieae, in which doubling of the endodermis occurs very early in ontogeny, taking place prior to the differentiation of the stelar elements. The remainder of the cortex consists of

six to eight layers of parenchymatous cells that are round in transection and two or three times as long as broad, with regular intercellular spaces.

The third histogen, the dermatogen-calyptrogen, gives rise to both epidermis and root cap. The manner of its division has been concisely described by Port,

"The cells of this layer by periclinal divisions perpetuate the histogen and form successive layers of root cap cells which may subsequently divide in one or more planes to keep pace with the growth of the root axis. The cells which form the proximal margin of the dermatogen-calyptrogen layer undergo a final periclinal division and each inner daughter cell then functions as an epidermal initial thereafter dividing only in anticlinal planes to form the epidermis. In this manner a uniseriate epidermis develops and the initiating layer is maintained."

At maturity, the primary root has a diarch radial protostele in which the two primary phloem groups lie on the flanks of the primary xylem strand and are separated from it by fundamental parenchyma which later functions as a procambial zone. The protoxylem points abut the pericycle which is surrounded by the uniseriate or partially biseriate endodermis. The cortical parenchyma is limited externally by an epidermis and there are numerous root hairs. (Fig. 335.)

SECONDARY THICKENING. — Secondary thickening of the root is initiated very early in ontogeny, in the zone of fundamental parenchyma lying between the primary phloem and xylem, and the production of secondary vascular tissues may occur in seedlings approximately eight days old. The secondary xylem consists of parenchyma and large vessels that are laid down in single or frequently double radial rows. The rows are separated by ray parenchyma and the diarch character of the primary xylem is evident even in older roots because of the development of two prominent pericyclic rays that extend toward the periphery on the same radii as the two protoxylem points. The vessel segments are three to four times as long as broad, the walls being densely pitted with oval or elliptical pits that have their longest dimension in the transverse plane. The elongated xylem parenchyma cells surrounding the vessels are at first thin-walled, but become lignified in mature roots. The ray parenchyma cells are isodiametric or sometimes elongated in the radial dimension.

The secondary phloem is comprised of groups of long, narrow sieve tubes and companion cells surrounded by larger parenchymatous cells. There are numerous latex tubes which consist of very slender cells arranged in longitudinal series and forming a continuous system owing to numerous cross anastomoses. (Fig. 334, C.) The latex ducts are relatively infrequent in the pericyclic tissue which surrounds the secondary phloem and forms the outermost zone of the root, and none occur in the secondary xylem. Latex branches may ramify through the pericyclic tissue interconnecting the latex tubes of adjacent phloem strands, and they also penetrate the pericycle together with the vascular tissue at points where lateral roots are diverged.

There is an early loss of the cortex and epidermis as a result of secondary thickening, and the outermost cells of the pericycle function as a phellogen forming the periderm. The primary pericyclic cells are rectangular in longisection, and may become much extended tangentially as cellular growth compensates for the increasing size of the axis.

VASCULAR TRANSITION. — Among the studies of vascular transition in the Compositae are those of Chauveaud (6), Lee (17), who investigated fifty species including *Lactuca sagittata* Waldst., Siler (24) on *Arctium minus* Bernh., and Phillips (21), who studied *Cynara Scolymus* L.

In *Lactuca sativa* L., Port (22) finds that the vascular transition agrees in general plan with that reported by Lee (17) for *L. sagittata*. The primary vascular system of the seedling axis, including the primary root, hypocotyl and cotyledons, is a continuous one which is distinct in its origin from that of the stem; but late in ontogeny the downwardly extended traces of the epicotyledonary leaves anastomose with the vascular strands of the hypocotyl. The vascular transition involves a rather short portion of the seedling axis. It begins in the upper third of the hypocotyl, and the complete endarch condition is attained about halfway up the midrib of the cotyledon.

The cotyledon has three main veins, a midrib and two small laterals. (Fig. 336, H.) In the distal portion of the cotyledonary blade, the bundles are endarch collateral, and the lateral ones remain so even to a point below the cotyledonary node. In the proximal portion of the cotyledon, the metaxylem of the midrib is differentiated laterally in relation to the protoxylem, forming a

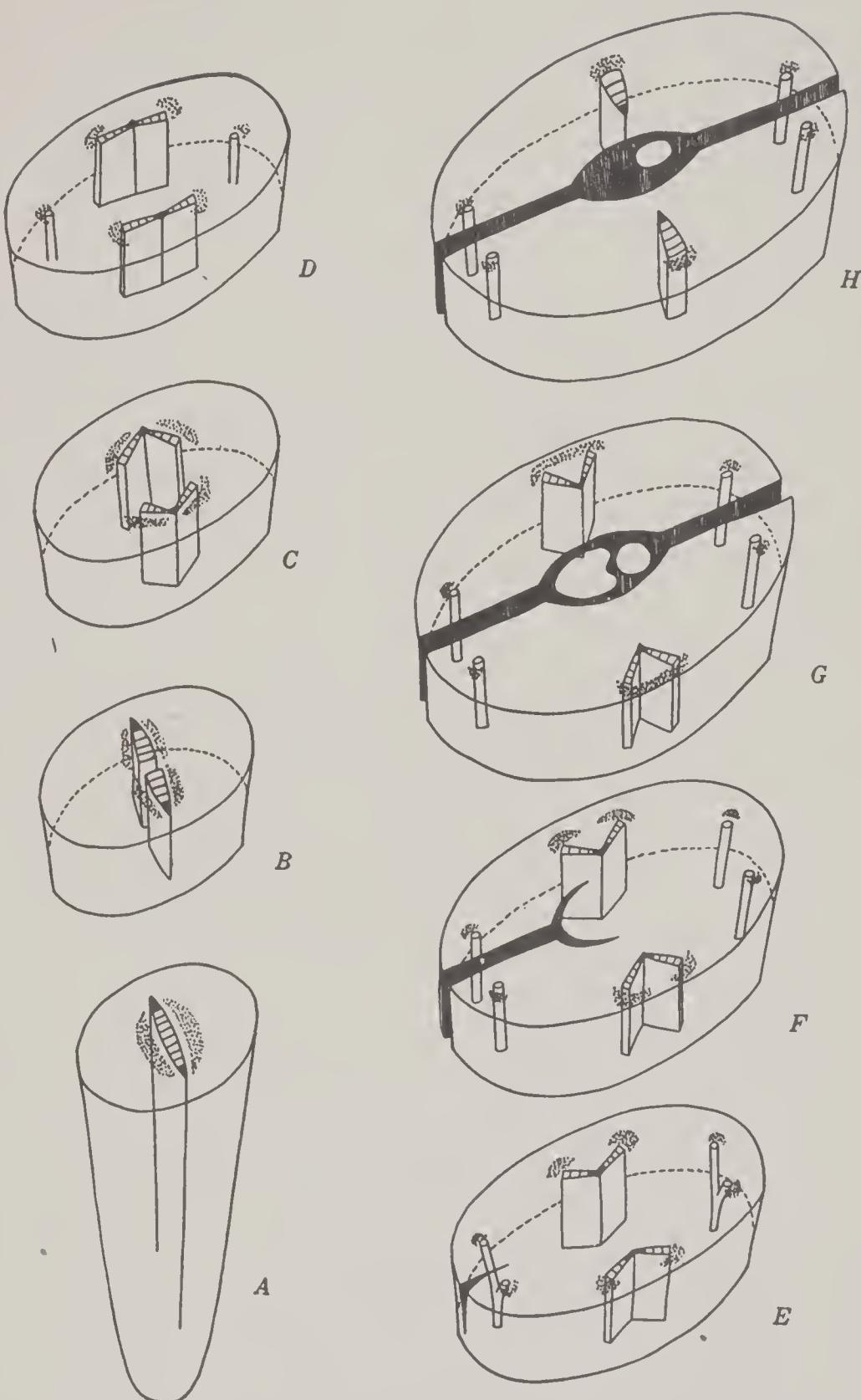


FIG. 336. A-H, successive levels in vascular transition in seedling axis, diagrammatic sectors based upon condition in seedlings six days old (description in text). The solid areas represent protoxylem, lined regions, metaxylem, and dots, primary phloem, variety New York Regular.

triad, as Compton (7) has termed it, in which the two metaxylem arms are tangentially oriented with respect to the protoxylem. (Fig. 336, G.) At about the level of cotyledonary divergence, the lateral orientation of the metaxylem is more marked; and, instead of a single group of phloem elements lying on the abaxial side of each bundle, there are two strands that are laterally placed and separated from each other by parenchymatous cells. (Fig. 336, E, F.)

Lower in the hypocotyl, the phloem is differentiated progressively in a more lateral position, and may form a varying number of distinct strands that are farther apart from one another than at any point higher in the seedling axis. At this level, the bundles occupy positions nearer the center of the hypocotyl, constituting the primary stele of the axis. Below the cotyledonary node, the opposed lateral bundles of the two cotyledons unite in pairs to form two small bundles which lie at right angles to the larger median bundles coming from the midribs of the cotyledons. (Fig. 336, E.) These laterals end blindly somewhat lower in the hypocotyl, but are later joined to the two large bundles by the development of secondary vascular tissue.

At about the level at which the lateral bundles terminate, the stelar pattern undergoes further change. The metaxylem arms of each bundle are differentiated in a lateral position so that they form a straight line with their respective protoxylem points. (Fig. 336, D.) The phloem groups lie closer to each other, and each bundle may be divided into two more or less distinct strands. Slightly below this point, the metaxylem is differentiated laterally and centripetally so that two tangentially exarch bundles are formed. (Fig. 336, C.)

Near the middle of the hypocotyl, the relation of protoxylem and metaxylem is strictly exarch. The diarch character of the stele is evident although there are still parenchymatous cells at the center of the axis separating the two halves of the xylem strand. At this point, the phloem is differentiated laterally in relation to the long axis of the xylem strand and forms two distinct groups. (Fig. 336, B.) In the lower part of the hypocotyl, the stele is similar to the primary root. (Fig. 336, A.)

THE COTYLEDONS. — The fleshy cotyledons are alike in structure but there may be considerable variation in their size and shape. They have wide bases and the most common form is spatulate

with a broadened apex which is frequently notched at its extreme tip. Lee (17) has observed that the venation of the cotyledons in the composites is characterized by two facts: (1) the main bundles never end blindly in the mesophyll, but anastomose with one another in the terminal portion of the blade; (2) the lateral bundles on either side of the mid-vein always unite with it at the apex of the cotyledon. Lettuce corresponds in this respect with the *Arctium* type in which there are two lateral veins and a midrib at the base of the cotyledon. The laterals follow the margins of the blade, uniting with the midrib at the apex of the cotyledon; and, in addition to them, two major branches of the midrib arise near the middle of the cotyledonary blade, pursue a course parallel to the laterals for some distance, and join them near the tip of the cotyledon. (Fig. 331, F.) All minor branches arising in the basal portion of the blade anastomose with one of the major veins at some point so that the venation constitutes a closed system.

The mesophyll of the fleshy blade consists of a palisade region a single layer in thickness, and a spongy zone of several layers. (Fig. 337, B.) The spongy cells adjacent to the palisade layer are frequently elongated in the same plane as the palisade cells so that they form a transitional type. As the cotyledon expands, the intercellular spaces enlarge and the mesophyll becomes porous. The vascular bundles are collateral, and neither Jean (12) nor Port (22) found any evidence of an inner phloem associated with them, such as is present in the stem and leaf. Lactiferous ducts occur on the abaxial face of the phloem and occasionally in the

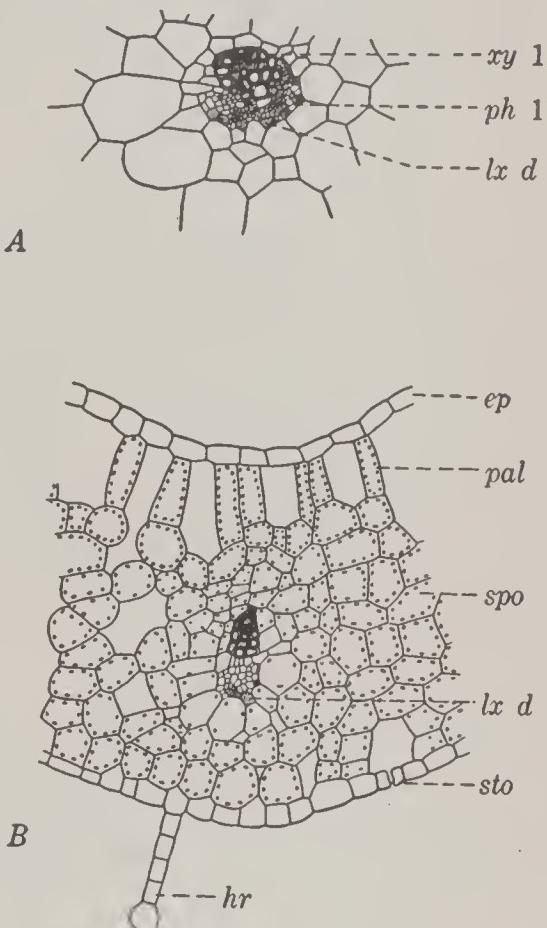


FIG. 337. A, transection of main vein near base of ten-day-old cotyledon showing location of lactiferous ducts; B, transection through portion of same cotyledon nearer apex of blade, variety New York Regular: *ep*, epidermis; *hr*, hair; *lx d*, lactiferous duct; *pal*, palisade; *ph 1*, primary phloem; *spo*, spongy tissue; *sto*, stoma; *xy 1*, primary xylem.

spongy zone of several layers. The vascular bundles are collateral, and neither Jean (12) nor Port (22) found any evidence of an inner phloem associated with them, such as is present in the stem and leaf. Lactiferous ducts occur on the abaxial face of the phloem and occasionally in the

phloem strand. These parallel the course of the bundles and are frequently interconnected by anastomoses and cross branches. (Fig. 334, A.)

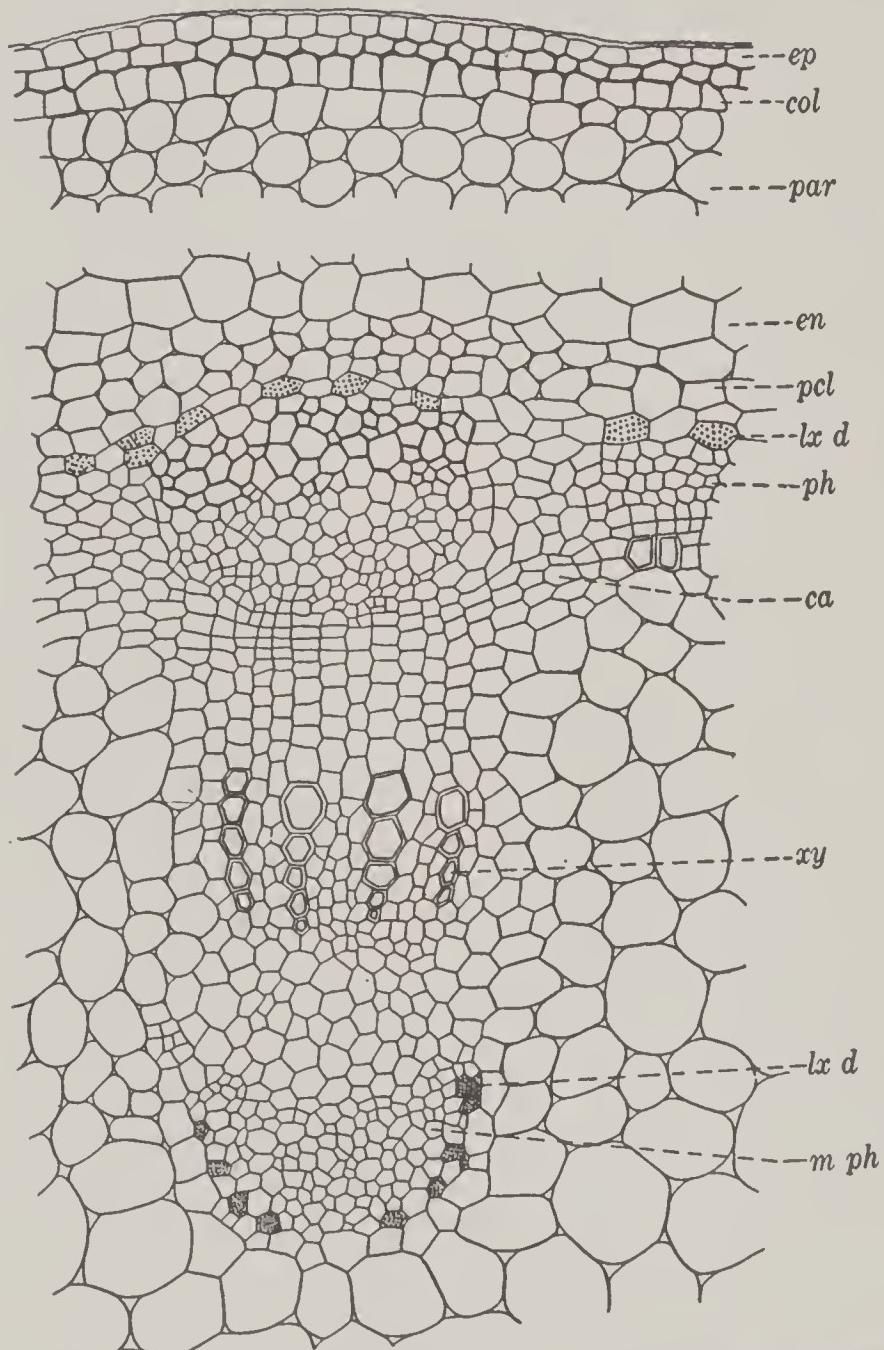


FIG. 338. Transection of portion of stem showing bundle and medullary phloem, a part of cortex is not shown, variety New York Special: *ca*, cambium; *col*, collenchyma; *en*, endodermis; *ep*, epidermis; *lx d*, lactiferous duct; *m ph*, medullary phloem; *par*, parenchyma; *pcl*, pericycle; *pb*, phloem; *xy*, xylem.

Stomata occur in both epidermal surfaces, the frequency being greater in the abaxial one. The epidermis is also characterized by multicellular epidermal hairs which consist of a single or double row of cells that are terminated by a capitate enlargement.

THE STEM. — In the early stages of its development, the stem does not undergo internodal elongation, and the leaves, which are diverged in a spiral phyllotaxy (commonly a $\frac{2}{5}$ arrangement), are crowded on the axis. As a result, either a head or a close rosette of basal leaves surrounds the crown stem, which becomes large and fleshy, owing to the pronounced increase in the parenchymatous tissue of the pith. Later in ontogeny, the seed stalk elongates and the buds in the axils of the upper leaves also expand so that a branching crown is formed which bears the inflorescences.

The young stem is round or oval and somewhat ridged below each node owing to the downwardly extending bundles of the leaf trace. The epidermis is glabrous except for occasional scattered hairs and contains numerous stomata in which the guard cells are usually oriented with their long axes parallel with that of the stem. The epidermal cells are irregular in outline, having their long dimension in the vertical plane, and the walls are curving as seen in surface view. In transection, they are square or rectangular and their outer surfaces are moderately cutinized. Within the epidermal layer are two or more rows of compact collenchymatous cells. The large parenchymatous cells of the cortex are loosely organized and are limited centripetally by the endodermis. This layer is differentiated from the other cortical tissues by the continuity of its cells, whose radial walls abut without intercellular spaces. (Fig. 338.)

The vascular tissue of the immature stem constitutes a dissected siphonostele, but the collateral bundles are soon connected, through the development of interfascicular cambium, and a continuous vascular cylinder is formed. The pericycle becomes multiseriate, and numerous lactiferous ducts develop in its inner

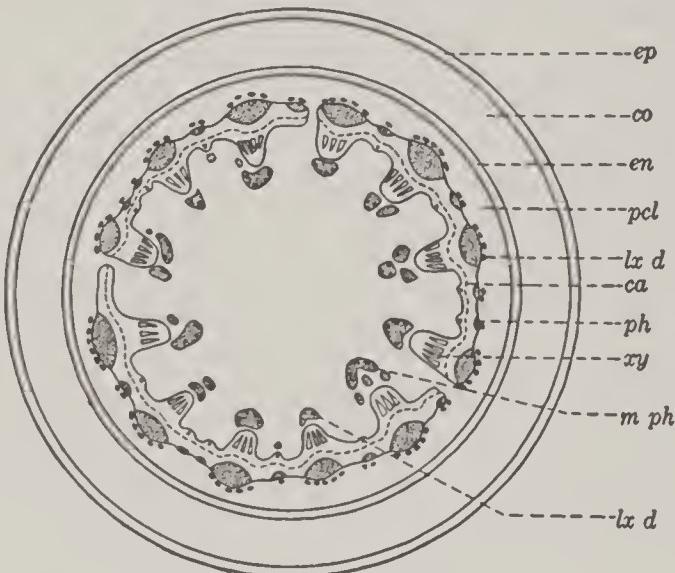


FIG. 339. Diagrammatic transection of partly mature floral axis showing arrangement of bundles, medullary phloem and distribution of lactiferous ducts, variety New York Special: *ca*, cambium; *co*, cortex; *en*, endodermis; *ep*, epidermis; *lx d*, lactiferous duct; *m ph*, medullary phloem; *pcl*, pericycle; *ph*, phloem; *xy*, xylem.

layer, especially in sectors adjacent to the phloem. (Fig. 339.) In addition to the ducts occurring in the pericycle, smaller ones are also found in the medullary phloem strands. They commonly develop around the inner periphery, but may extend through the central portion of the phloem, and similar ducts sometimes occur in the outer phloem. The primary vascular elements of the bundle are annular-spiral or spiral, the latter type frequently forming walls with double spiral thickenings. Slender, elongated parenchymatous cells separate the vessels from each other. The secondary vessels are large and angular with transversely elongated pits which sometimes give the vessel segments the appearance of being scalariform or reticulate.

MEDULLARY BUNDLES. — Medullary phloem strands appear in the pith centrad to the primary xylem so that the bundles may appear to be bicollateral. However, the late development of the medullary phloem strands, in addition to the fact that their arrangement and the number of strands adjacent to a bundle may vary, indicates that these units do not constitute an integral part of the vascular bundle.

With respect to this situation Solereder (25) has pointed out that in the Cichorieae there may be medullary vascular bundles formed by the addition of xylem to the phloem. This was observed by Petersen (20), who noted intraxylary phloem in *Lactuca* and described the occurrence of some xylem in connection with this tissue. Weiss (30) also investigated this matter and demonstrated that the chief bundles of the vascular system which have inner phloem associated with them are not true bicollateral bundles. Specifically referring to *L. sativa*, he stated that the medullary phloem is directly continuous with the leaf trace in some instances, and that the small lateral phloem strands adjacent to the protoxylem groups are direct continuations of strands arising on the adaxial face of the leaf bundle. Other phloem strands were found to pass into the pith as branches from the outer phloem of the stem bundle, so that they could be regarded as being only indirectly connected with leaf traces. Kruch (16) also investigated this group extensively, and concluded that the medullary strands might be direct continuations from the phloem associated with leaf or branch traces. In a few cases, including *Lactuca*, there are both foliar and caudine strands.

Worsdell (31), having studied medullary phloem in the Com-

positae from the standpoint of its phylogenetic implications, confirmed the work of previous investigators with respect to the course of the strands in the stem of *Lactuca sativa* and *L. virosa*. His summation follows:

"Medullary strands occur throughout the stem. In the higher part of this organ phloem-strands only occur. In the basal region they acquire xylem and become bundles. In this basal region, at a still lower level, they lose the xylem, and eventually either die out *in situ* or join the vascular ring. The amount of xylem in the medullary strands varies with the thickness of the stem, and is always secondary in origin. The fate of the strands, if traced upwards, is fourfold. Some of them end blindly in the pith. Some pass into the vascular ring. Others pass out to form the medullary system of a branch; but in one and the same plant the branch-system may arise both in this way and also *de novo* in its pith-tissue. The small peripheral phloem-strands persisting in the higher part of the stem and peduncle become part of the ordinary vascular system of the flowers."

THE LEAF. — The gross morphology and the differences which exist between the leaves of lettuce varieties have been pointed out. In the New York variety, the sessile and somewhat auriculate, clasping leaves of the floral axis have a central vascular region which is thickened and concave on its adaxial surface. The principal veins extend through this fleshy region parallel to one another with occasional cross-connections occurring between the lateral members and the central bundle. From the lateral veins of this parallel series, branches extend outward to the periphery of the blade in a pinnate arrangement. These in turn branch and rebranch, forming a fine net-veined system in which some of the ultimate veinlets end in small islands in the leaf blade while others terminate in the marginal teeth. In the basal leaves of the heading and bunching types, the principal veins are spreading and palmately arranged; but even the basal leaves of the Cos type have a prominent midrib and a pinnate system of venation.

Except in the region of the midrib and of the major laterals, the blade is thin. The epidermal cells of both upper and lower surface are extremely sinuous as seen in surface view, except for those which lie over the principal veins where the cells are elongated with oblique or somewhat pointed ends. These regions also differ from the remainder of the epidermal surface in that there are few stomata. Elsewhere they occur in large numbers and in about equal frequency on both surfaces. As pointed out

by Eames and MacDaniels (9), the guard cells belong to the type in which the wall is unevenly thickened and the exposed margins of the two cells project as thickened ridges. (Fig. 340, B.) Epidermal hairs occur at the margin of the leaf between the teeth, and also along the veins. These are numerous in young leaves but break up and wither as they mature. The hairs are multicellular and usually capitate, the column consisting of either a single or double row of cells arising from one or two short basal epidermal cells.

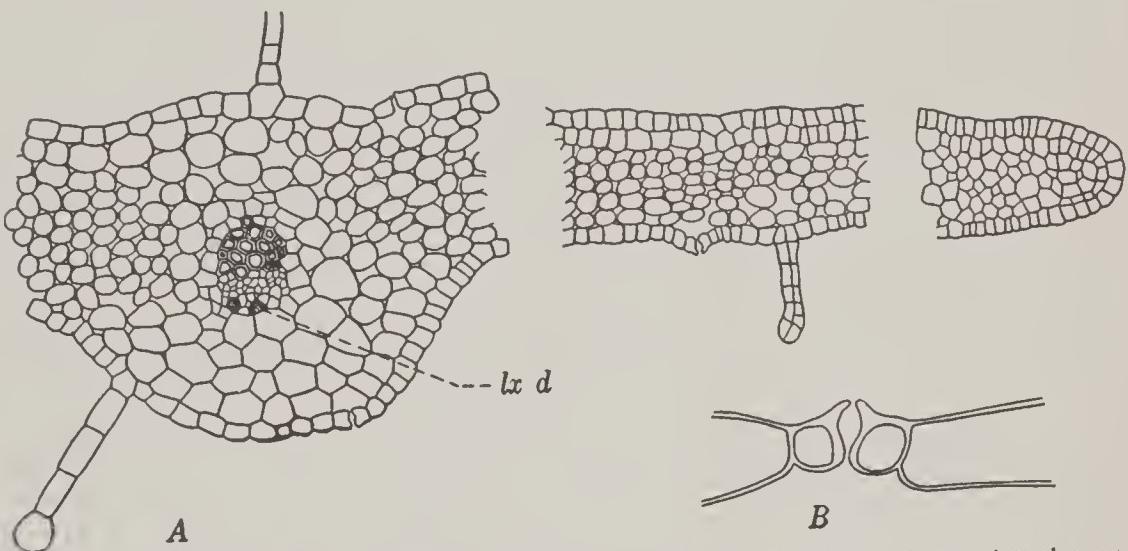


FIG. 340. A, transections of segments of young foliage leaf 12 days old showing character of mesophyll, development of hairs and lactiferous ducts, $lx d$; B, side section of stoma and guard cells, variety New York Regular.

The mesophyll is uniform; and, in the young leaf, the parenchymatous cells which comprise it are approximately isodiametric and rather compactly arranged. (Fig. 340, A.) As the leaf enlarges, the mesophyll becomes more porous and large intercellular spaces are formed. Even at maturity, there is little or no differentiation of the mesophyll into a palisade and spongy region, the chief difference between the adaxial and abaxial cells being that the former are somewhat more compact, while the latter tend to elongate in a plane parallel to the flat surface of the blade. The distribution of chlorophyll is variable, depending upon the variety as well as upon the position of the leaf. In the heading types, many of the inner leaves are practically devoid of pigment, while in leafy types and in the leaves arising on the floral axes, chlorophyll is present in the guard cells and in all of the parenchyma of the mesophyll with the exception of the cells adjacent to the veins. These usually have no chlorophyll although those

immediately abutting the vein may have a few plastids. There may also be small plastids in the xylem parenchyma of the larger veins.

The main bundles are collateral, but there are strands of adaxial phloem which follow the course of the bundles and extend into the medullary region of the stem. Lactiferous ducts occur around the periphery of the abaxial phloem and there may be similar ducts lying in the same relation to the adaxial phloem. The primary xylem elements are chiefly of the spiral type. The larger bundles develop a cambium and the secondary xylem vessels are similar to those of the stem. The smaller veins do not have strands of adaxial phloem associated with them and the ultimate veinlets consist of single tracheids.

LACTIFEROUS DUCTS. — The presence of lactiferous ducts has been noted in descriptions of the various organs of the plant, but they are sufficiently characteristic to warrant a summary of their occurrence and distribution. The development of articulated lactiferous ducts in the Cichorieae has long been known and frequently investigated. The early research on this point has been summarized by de Bary (2) and Scott (23), and the latter has described the origin and ontogeny of the ducts for a member of this tribe. When the ducts occur in primary tissues, they arise early in the ontogeny of the plant and are probably differentiated during the embryogeny in many instances. Scott observed their formation in the seedling during the initial stages in germination. The ducts at first consist of a longitudinal series of cells which have definite end walls. Later in ontogeny, they become continuous, non-septate passages owing to the perforation and resorption of the end walls, as well as to the occurrence of frequent cross anastomoses between adjacent ducts which form connecting canals. Solereder (25) has pointed out that the

"tubes of the stem and leaf form a special system of their own, which is distinct from the lactiferous system of the root," but notes that "the primary lactiferous system of the root is however connected with the primary system of the stem, for at a certain level both systems are found to be present in a transverse section and united with one another by anastomoses."

Summing up the situation for *Lactuca*, it has been noted that the lactiferous ducts occur in the primary tissues of the root, where they form an arc outside the primary phloem in the peri-

cycle; and they may also occur on the inner face of the primary phloem. Both types may develop in young seedlings before the protoxylem is differentiated. In the secondary tissues of the root, the lactiferous ducts appear in the phloem parenchyma, and branches frequently extend through the pericyclic parenchyma adjacent to the phloem. (Fig. 334, C.)

In the hypocotyl, ducts appear adjacent to the primary phloem as in the root, and may occur also in the hypodermal region of the cortex. In the cotyledons, they lie along the abaxial surface of the phloem and extend into the mesophyll. In the stem, ducts are present in the pericyclic arcs outside the outer phloem, and, to a lesser degree, in the outer phloem. They are also found on the centrad surface of the medullary phloem strands and are reported by de Bary as ramifying into these strands. In the leaf, the latex ducts occupy the same position with respect to the phloem as in the cotyledon, and branches extend into the mesophyll. In the inflorescence, de Bary has noted that the latex tubes accompany the bundles of the floral traces.

Solereder reports that lactiferous hairs have been observed on involucral and other bracts in the genus *Lactuca*, and that there is an excretion of latex when the involucral leaves are touched. The lactiferous hairs together with two or more basal epidermal cells become united with the free ends of branches of the lactiferous system which accompany the vascular bundles. This is accomplished by the absorption of portions of the intervening walls so that the hairs actually represent terminations of the lactiferous system.

OIL DUCTS. — Oil ducts have been reported by van Tieghem (28) for many species in the series *Tubuliflorae*, but they are usually lacking in the *Liguliflorae*, which includes the tribe *Cichorieae* and the genus *Lactuca*. Exceptions have been reported in the roots of *Scolymus* by van Tieghem, and in *Cynara* by Phillips (21), where oil ducts are located between the two layers of a double endodermis. These two forms are apparently exceptional cases in which true oil passages as well as lactiferous ducts occur. Rudimentary oil passages in the diarch primary roots of *Cichorium intybus* and *Lampsana communis* have been reported by de Bary. Port found a somewhat similar situation in *Lactuca sativa* where intercellular spaces develop between adjacent layers of cortical cells; but, as in *Cichorium*, no contents were observed.

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GLOSSARY

- ✓**ABAXIAL**, the side of a lateral organ away from the axis.
- ACHENE**, see *Akene*.
- ACROPETAL**, applied to structures that are produced in succession toward the apex.
- ACTINOMORPHIC**, (of flower) arrangement of floral parts in a regular pattern capable of bisection into similar halves in two or more planes.
- ACUMINATE**, with a tapering end.
- ✓**ADAXIAL**, the side of a lateral organ next the axis.
- ADNATE**, united, as an inferior ovary with the calyx tube.
- ADVENTITIOUS**, (of roots) those that arise from any structure other than a root; (of buds) those that arise other than as terminal or axillary structures.
- AGGREGATE FRUIT**, a collection of the separate carpels of one flower, *i.e.*, raspberry.
- AKENE**, a small, dry, hard, one-celled, one-seeded, indehiscent fruit consisting of one carpel (buttercup), or more than one with adnate calyx (composites).
- AMPHICRIBRAL**, (of bundles) with the phloem completely surrounding the xylem.
- AMPHIPHLOIC**, (of steles) with the phloem outside of and also centrad to the xylem cylinder.
- AMPHITROPOUS**, see *Hemitropous*.
- AMPHIVASAL**, (of bundles) with the xylem completely surrounding the phloem.
- ANASTOMOSIS**, union of one vein or bundle with another.
- ANATROPous**, (of ovules) one in which the nucellus is inverted and straight, with the micropyle adjacent to the hilum.
- ✓**ANDROECIUM**, the stamens considered collectively.
- ANISOCARPIC**, (of flowers) with the number of carpels less than the number of parts in the other floral sets.
- ANNUAL**, with a life cycle of one year's duration.
- ANNULAR**, (of conductive elements) with secondary wall thickenings in the form of rings.
- ANTERIOR**, placed in the front; remote from the axis of an inflorescence.
- ✓**ANTHER**, the portion of the stamen containing the pollen, usually bilocular.
- ANTHESIS**, the time of floral expansion.
- ANTICLINAL**, at right angles to the surface; (of walls) those which cut the surface or periclinal walls at right angles.
- ANTIPODAL**, (cells or nuclei) those which occupy the chalazal end of the megagametophyte.
- APETALOUS**, without petals.
- APICAL**, at the point or summit of a structure.
- ARCHESPORIUM**, the cell or cells from which wall tissue, if any, and the sporogenous tissue are derived in the micro- or megasporangium.
- ATROPOUS**, see *Orthotropous*.
- AURICULATE**, possessing ear-shaped appendages (auricles).
- AWN**, a bristle-shaped appendage, as on the glumes of many grasses.
- AXIL**, the angle subtended by the stem axis and a leaf or branch.

GLOSSARY

- AXILE**, located on the axis, *i.e.*, axile placentation.
- Axis**, the central line of any organ or the support of a group of organs; a stem, root, etc.
- BASIPETAL**, applied to structures that are produced in succession toward the base.
- BAST**, phloem, sometimes the inner fibrous portion of the bark.
- BERRY**, a fleshy fruit derived from a superior ovary consisting of one or, more often, two or more carpels.
- BICOLLATERAL**, (of bundles) having phloem on the outer and inner faces of the xylem.
- BIENNIAL**, with a life cycle of two years' duration.
- BLADE**, the expanded portion of the leaf, lamina.
- BORDERED PIT**, a pit in which the margin projects over the closing membrane.
- BRACT**, a specialized leaf type commonly subtending a flower or an inflorescence, sometimes caudate.
- BUD**, an unelongated stem tip with its lateral members.
- BULB**, a bud with fleshy leaves, usually subterranean.
- BULLIFORM CELLS**, large, thin-walled epidermal cells which occur in certain grasses, *i.e.*, corn.
- CADUCOUS**, falling off early.
- CALLUS**, (of sieve tube) a deposit on the sieve plates.
- CALYPTROGEN**, the layer or histogen from which the root cap is derived.
- CALYX**, the outermost cycle of floral parts, the sepals considered collectively.
- CAMBIUM**, a lateral meristem which produces secondary xylem and phloem.
- CAMPYLOTROPOUS**, (of ovules) one in which the nucellus is curved and the chalaza and micropyle are in a plane at right angles to the funiculus.
- CAPILLARY**, slender, hairlike.
- CAPITATE**, shaped like a head.
- CAPSULE**, a dry, dehiscent fruit composed of more than one carpel and sometimes involving a portion of the axis.
- CARPEL**, a simple pistil, or a member of a compound pistil; a megasporophyll.
- CARPOPHORE**, (in Umbelliferae) a slender extension of the floral axis which supports the two pendulous mericarps.
- CARYOPSIS**, a fruit developing from a carpel in which the pericarp is adnate to the single seed.
- CASPARIAN STRIP**, a secondary thickening which develops on the radial and end walls of some endodermal cells.
- CATAPHYLL**, bud scales, also applied to the scales on rhizomes and cotyledons.
- CAULINE**, pertaining to the stem; (of bundles) those which have no direct connection with the common bundles that pass into the leaves.
- CELL**, a protoplast which usually consists of a nucleus, cytoplasm, and various inclusions; also applied to the cell wall.
- CENTRAL CYLINDER**, the vascular system of an axis; the stele.
- CENTRIFUGAL GROWTH**, from the center outwards.
- CENTRIPETAL GROWTH**, from the periphery towards the center.
- CHALAZA**, the point in an ovule or seed where the integuments diverge from the nucellus.
- CHLOROPLAST**, a plastid containing chlorophyll.
- CHONDRIOSOMES**, minute bodies in the cytoplasm having the form of granules, rods, or threads.
- CHROMOPLAST**, a plastid containing pigment.

- CILIATE, fringed with hairs.
- COLEOPTILE, (in Gramineae) the first leaf above the cotyledon which encloses the stem tip.
- COLEORHIZA, the sheath which surrounds the primary root in the embryo of the grasses.
- COLLATERAL, (of bundles) having the xylem and phloem side by side on the same radius.
- COLLENCHYMA, elongated, parenchymatous cells with variously thickened walls, commonly at the angles.
- COLLET, applied to the imaginary boundary between the aboveground and subterranean portions of a seedling axis.
- COMMISSURE, (in Umbelliferae) the adherent faces of the two carpels.
- COMMON BUNDLE, one that is common to both stem and leaf and continuous from one to the other.
- COMPANION CELL, a phloem element associated with a sieve tube and usually derived from a common mother cell.
- COMPLEMENTARY CELLS, loosely arranged cells which occur in the lenticel.
- COMPOUND, (of leaf) one in which the blade is divided into separate leaflets.
- CONJUNCTIVE TISSUE, non-vascular tissue adjacent to bundles which consists of lignified, usually elongated, cells.
- CONNATE, united.
- CONNECTIVE, that portion of the stamen which joins the two cells of the anther.
- CONNIVANT, convergent or coming into contact.
- CONVOLUTE, with one part rolled up longitudinally in another, as the petals of cotton.
- CORDATE, heart-shaped.
- CORM, an enlarged, solid fleshy base of a stem, *i.e.*, Cyclamen or Indian Turnip.
- COROLLA, the inner cycle of the perianth; the petals considered collectively.
- CORPUS, the inner core of the growing point of the apex of the shoot
- Cortex, that portion of an axis between the epidermis and the stele.
- CORYMB, a flat-topped flower cluster, arranged as a raceme, in which the flowers develop centripetally.
- COTYLEDONS, the first leaves of the embryo.
- CRENATE, (of leaves) dentate with rounded teeth.
- CULM, the stem of the grasses.
- CUTICLE, a non-cellular deposit of cutin on the surfaces of epidermal cells, occasionally on the subepidermal ones.
- CYMB, a determinate flower cluster in which the central or terminal flowers bloom first.
- CYSTOLITH, a concretion of calcium carbonate which occurs on an outgrowth of the cellulose wall, *i.e.*, some epidermal cells of Cannabis.
- CYTOPLASM, the more or less transparent, viscous, colorless substance which with the nucleus constitutes the protoplast of a cell.
- DECIDUOUS, (of leaves) not persistent, falling in season.
- DECOMPOUND, several times divided or compounded.
- DECUMBENT, reclining with an ascending summit.
- DECURRENT, (of a leaf) extending down the stem below the node.
- DECUSSATE, (of leaves) an opposite arrangement with the pairs alternating at right angles.
- DEHISCENT, opening by means of pores, valves, slits, etc., as in a capsule or an anther.
- DENTATE, toothed.
- DERMATOGEN, the layer or histogen from which the epidermis is derived.

- DIADELPHOUS**, (of stamens) arranged or combined into two sets.
- ✓ **DIARCH**, (of root) a stele with two protoxylem groups.
- DICHOTOMOUS**, forking regularly by pairs.
- DICOTYLEDONOUS**, having two cotyledons.
- ✓ **DICTYOSTELE**, a vascular cylinder or stele consisting of distinct bundles; a dissected siphonostele.
- DIGITATE**, (of leaves) with the leaflets arising at the apex of the petiole.
- DIMEROUS**, having all the parts in twos.
- ✓ **DIOECIOUS**, with staminate and carpellate flowers on separate plants.
- DISTICHOUS**, in two vertical ranks, as the leaves of grasses.
- DORSAL**, relating to the back or outer surface of an organ.
- ✓ **DRUPE**, a fruit developed from a single carpel with a fleshy exocarp and a hard stony endocarp or pit usually containing a single seed. Less exactly applied to stone fruits that are multi-carpellate with one to several seeds.
- DUCT**, an elongated cell or a multicellular cavity; a gland.
- ECTOPHLOIC SIPHONOSTELE**, a stele in which there is a zone of phloem outside the xylem but no inner phloem.
- EMBRYO**, a rudimentary plant.
- EMERGENCE**, a surface outgrowth arising from a few superficial layers, i.e., prickles.
- ✓ **ENDARCH**, applied to primary xylem in which the progressive development of the elements is centrifugal.
- ✓ **ENDOCARP**, the inner layer of the pericarp or fruit coat.
- ✓ **ENDODERMIS**, the innermost layer of the cortex which abuts the stele.
- ✓ **ENDOGENOUS**, produced within from deep-seated tissues instead of from superficial layers.
- ✓ **ENDOSPERM**, the nutritive tissue occurring within the seed which is derived from the triploid endosperm nucleus.
- ENDOTHECIUM**, inner lining of the locule of an anther.
- ENTIRE**, (of leaves) without dentation or division.
- EPHEMERAL**, short-lived, usually lasting but a day.
- EPIBLAST**, a lateral outgrowth from the embryonic axis of some grasses.
- EPICARP**, the outer layer of the pericarp or fruit coat.
- EPICOTYL**, that portion of the seedling axis above the cotyledonary node.
- EPIDERMIS**, the superficial layer of cells covering a plant.
- EPIGEAL**, (of cotyledons) expanding above the soil surface.
- EPIGYNOUS**, (of flowers) with all floral parts conjoint and generally divergent from the ovary at or near its summit.
- ETIOLATE**, deprived of color or lengthened owing to the exclusion of light.
- ✓ **EXARCH**, applied to primary xylem in which the progressive development of the elements is centripetal.
- ✓ **EXOCARP**, the outer layer of the pericarp or fruit coat.
- EXOGENOUS**, arising from superficial tissues.
- FASCICULAR CAMBIVM**, the cambium which gives rise to the secondary vascular tissues of a bundle.
- FIBER**, an elongated, thick-walled mechanical element.
- FILAMENT**, the part of the stamen supporting the anther.
- FLORAL ENVELOPE**, the perianth (calyx and corolla).
- FLOWER**, a shoot beset with sporophylls (stamens and carpels).
- FOLLICLE**, a dry fruit consisting of a single carpel which dehisces along the ventral suture.

- FRUIT**, (of angiosperms) the mature ovary and any associated parts.
- FUNICULUS**, the stalk of an ovule or seed.
- FUSIFORM**, spindle-shaped, tapering at both ends.
- GAMETE**, a reproductive cell which by union with another gamete produces a zygote. Cf. *Microgamete*, *Megagamete*.
- GAMOPETALOUS**, having more or less un-diverged or "united" petals.
- GAMOSEPALOUS**, having more or less un-diverged or "united" sepals.
- GLABROUS**, smooth, without hairs or pubescence.
- GLAND**, a secreting structure or surface.
- GLAUCOUS**, covered with a bloom.
- GLUME**, a chaffy bract occurring at the base of the spikelet in grasses.
- GRAIN**, see *Caryopsis*.
- GROUND TISSUE**, applied to the fundamental parenchyma — pith, medullary rays, and cortex.
- GYNOECIUM**, the pistil or pistils of the flower, the carpels considered collectively. (Also *gynoecium*.)
- HABIT**, the general appearance of a plant.
- HEAD**, an inflorescence of sessile or sub-sessile flowers on a very short axis or receptacle.
- HEMITROPOUS**, (of ovules) applied when the ovule is inverted with a straight nucellus and the micropyle and chalaza are at right angles to the funiculus.
- HESPERIDIUM**, a berry of the type found in citrus fruits.
- HILUM**, the scar or point of attachment of the seed.
- HISTOGEN**, regions or layers of meristematic tissue from which primary tissues are derived. Cf. *Dermatogen*, *Periblem*, etc.
- HYALINE**, translucent or transparent.
- HYDATHODE**, a pore or organ concerned with the exudation of water.
- HYPOCOTYL**, the portion of the seedling axis below the cotyledonary node.
- HYPODERMIS**, applied to the cells immediately under the epidermis which may be supportive or protective in function.
- HYPOGEAL**, (of cotyledons) remaining underground.
- HYPOGYNOUS**, (of flowers) with the sepals, petals, and stamens free from and divergent below the ovary.
- HYPOPHYSIS**, the cell or cells resulting from the transverse division of the cell next adjoining the suspensor cell, and giving rise to the tip of the root.
- IMBRICATE**, overlapping vertically or spirally.
- INCLUSIONS**, (of cell) applied to bodies occurring in the cytoplasm; non-protoplasmic substances in the form of granules, droplets, crystals, etc.
- INDEHISCENT**, (of fruits) remaining closed at maturity.
- INFERNIOR**, (of ovary) applied when there is conjoint growth of ovary wall and other floral parts, i.e., in epigynous flowers.
- INFLORESCENCE**, the arrangement of the flowers of a plant; more specifically, the flower cluster itself.
- INITIAL OR INITIALS**, a cell or group of cells from which a structure is developed or derived.
- INTEGUMENT**, (of ovule) a covering layer, later becoming a part of the seed coat.
- INTERCALARY**, (of meristem) applied to meristematic zones that are not apical, basal, or lateral, i.e., the intercalary meristem at the base of an internode in many grasses.
- INTERNODE**, the portion of the stem between two nodes.

GLOSSARY

- INTRORSE**, turned inward or toward the axis.
- INVOLUCEL**, a secondary involucre, as that occurring on the umbellet in some umbellifers.
- INVOLUCRE**, a cycle of bracts subtending a flower cluster, head, or single flower.
- IRREGULAR**, (of flowers) with the parts of a floral set of unequal size and shape; zygomorphic.
- ISOCARPIC**, with the number of carpels equal to that of the parts of other floral sets.
- KARYOLYMPH**, the hyaline fluid or sap occurring in a nucleus.
- KEEL**, the two anterior, united petals of a papilionaceous flower.
- KEY FRUIT**, see *Samara*.
- LACUNA**, an air-space in a tissue.
- LAMELLA**, a thin, flat plate or membrane. Cf. *Middle lamella*.
- LAMINA**, see *Blade*.
- LANCEOLATE**, narrow and tapering at both ends, usually broadest above the base and narrowed to the apex.
- LATEX**, a white or yellow viscous emulsion.
- LEAFLET**, one of the divisions of a compound leaf.
- LEAF TRACE**, a bundle which extends to a leaf; or, more inclusively, the complex of all the bundles that supply a single leaf.
- LEGUME**, the dry, dehiscent fruit of leguminous plants developed from a single carpel and usually opening along both sutures.
- LEMMA**, (in grasses) the lower of two bracts enclosing the flower, sometimes called the flowering glume.
- LENTICEL**, a corky area of loosely arranged cells in the periderm.
- LEUCOPLAST**, a colorless plastid.
- LIANA**, a climbing or twining plant.
- LIGULE**, a thin, scarious projection arising at the top of the leaf-sheath in grasses.
- LIMB**, the expanded portion of a gamopetalous corolla, or of a petal or leaf.
- LININ**, the substance comprising the reticulum of the nucleus.
- LOCULE**, one of the chambers in an anther or an ovary.
- LOCULICIDAL**, dehiscence of the locule of an ovary along the dorsal suture. Cf. *Septicidal*.
- LODICULES**, the small scales outside the stamens in the grass flower.
- LUMEN**, (of cell) the cavity bounded by the cell walls.
- LYSIGENOUS**, applied to a cavity formed by the disintegration and dissolution of cells. Cf. *Schizogenous*.
- MEDULLA**, the pith.
- MEGAGAMETE**, the larger of two uniting cells or gametes; the egg.
- MEGASPORANGIUM**, a sporangium in which the megasporangia are developed.
- MEGASPORE**, a tetraspore from which the megagametophyte develops.
- MEGASPOROPHYLL**, (in angiosperms) a carpel.
- MERICARP**, one of the akene-like carpels of the schizocarp of umbellifers.
- MERISTELE**, a stele in which the vascular bundles are distributed throughout the axis, i.e., corn.
- MERISTEM**, a group of embryonic cells whose derivatives may differentiate into various cell types and tissues.
- MESARCH**, applied to primary xylem in which the protoxylem is centrally located and the development of the metaxylem is both centripetal and centrifugal.
- MESOCARP**, the middle layer of the pericarp.
- MESOPHYLL**, the parenchymatous tissue between the adaxial and abaxial epidermis of the blade.

- METAPHLOEM**, the later-formed elements of the primary phloem.
- METAXYLEM**, the later-formed elements of the primary xylem usually characterized by reticulate or pitted walls.
- MICROGAMETE**, the smaller of two uniting cells or gametes, the sperm.
- MICROPYLE**, the orifice leading through the integuments to the nucellus. This frequently persists in the seed.
- MICROSPORANGIUM**, a sporangium in which microspores are developed.
- MICROSPORE**, a tetraspore from which the microgametophyte develops.
- MICROSPOROPHYLL**, (in angiosperms) a stamen.
- MIDDLE LAMELLA**, the isotropic intercellular substance between two primary walls.
- MONADELPHOUS**, (of stamens) forming a single cycle with undiverged filaments.
- MONOECIOUS**, with staminate and carpellate flowers on the same plant.
- MONOPODIAL**, applied to a stem with a single continuous axis.
- MULTIPLE FRUIT**, one developed from a cluster of flowers.
- NAPIFORM**, turnip-shaped.
- NECTARY**, an organ or surface where nectar is secreted.
- NODE**, the point on a stem from which a leaf diverges.
- NUCELLUS**, the body of an ovule, distal to its integuments.
- NUCLEOLUS**, a small proteinaceous body occurring in the nucleus.
- NUCLEUS**, a specialized often more or less ovoid or spherical portion of the protoplast surrounded by a delicate membrane, consisting of chromatin variously arranged, nuclear sap, and nutritive substances. It is essential in metabolism, growth, reproduction, and in the transmission of the determiners of hereditary characters.
- NUT**, a fruit resembling an akene but with a thick hard pericarp, usually developed from a compound ovary.
- OBCORDATE**, inverted heart-shaped.
- OBLATE**, flattened at the poles.
- OBOVATE**, inverted ovate.
- ONTOGENY**, the developmental history of an individual as contrasted with a race. Cf. *Phylogeny*.
- OPPOSITE**, (of leaves) two at one node.
- ORBICULAR**, circular.
- ORTHOTROPous**, (of ovule) one in which the nucellus is erect with the micropyle farthest from the hilum, in a straight line with it and the chalaza; also called *atropous*.
- OVARY**, the part of the carpel, or carpels in a compound pistil, that contains the ovules.
- OvATE**, egg-shaped with the broader end downward.
- OVULE**, the nucellus and its integuments.
- PALEA, OR PALET**, (in grasses) the upper bract which with the lemma encloses the flower.
- PALISADE**, the perpendicularly elongated cells which commonly form the layer of chlorenchyma beneath the adaxial epidermis of a leaf.
- PALMATE**, (of leaves) radiately lobed or divided.
- PANICLE**, a compound raceme.
- PAPILIONACEOUS**, (of corolla) with a standard, keel, and wings as in many leguminous plants.
- PAPPUS**, (in composites) the limb of the calyx which may be capillary, bristle-like, chaffy, or wanting.
- PARENCHYMA**, simple, non-specialized vegetative tissue with more or less isodiametric, thin-walled cells containing functional protoplasts.
- PARIETAL**, (placentation) that type in which the ovules are borne on the ovary wall.

- PASSAGE CELLS, the thin-walled endodermal cells which commonly lie on the same radii as the protoxylem strands.
- PECTINATE, (of a vascular system) applied where two series of vascular bundles alternate with each other as the teeth of two combs.
- PEDICEL, the supporting axis of a single flower.
- PEDUNCLE, the supporting axis of a single flower or a flower cluster.
- PENTACYCLIC, (of flower) with five whorls of floral parts.
- PENTAMEROUS, with parts in fives, as a calyx of five sepals.
- PENTARCH, (of root) a stele with five protoxylem groups.
- PEPO, a fruit developed from an epigynous flower in which the tissue of the receptacle surrounds the pericarp, forming a more or less hardened rind as in cucurbits.
- PERENNIAL, with a life cycle of more than two years' duration.
- PERFECT, (of flower) having both stamens and carpels.
- PERIANTH, the floral envelope comprised of the calyx and corolla (if present) regardless of their form.
- PERIBLEM, the layer or histogen from which the cortex is derived.
- PERICARP, the mature ovary wall.
- PERICLINAL, curved in the same direction as the surface or circumference; (of walls) those which are parallel with the surface.
- PERICYCLE, the outermost cell-layer of the stele lying adjacent to the endodermis, frequently becoming a multi-layered zone.
- PERIDERM, the outer protective layer in older axes, consisting of the phellogen and its derivative tissues, phellem and phelloderm.
- PERIGYNOUS, (of flowers) applied when there is conjoint growth of the outer cycles of floral parts distinct from the
- carpel or carpels and divergent below them.
- PERIPHERAL, on or near the margin.
- PETAL, one of the members of the corolla.
- PETIOLE, the supporting stalk of a leaf.
- PHELLEM, cork tissue.
- PHELLODERM, cells cut off centripetally by the phellogen.
- PHELLOGEN, a lateral meristem that cuts off phelloderm and phellem; the cork cambium.
- PHLOEM, a complex vascular tissue which may include sieve tubes, companion cells, fibers, parenchyma, and secretory cells.
- PHYLLOTAXY, the mode in which leaves are arranged on the stem axis.
- PHYLOGENY, the developmental history of a race rather than an individual. Cf. *Ontogeny*.
- PISTIL, a carpel or group of undiverged carpels, commonly subdivided into stigma, style, and ovary.
- PITH, the central parenchymatous portion of the axis; the medulla.
- PLACENTA, the surface in an ovary that bears the ovules.
- PLASMODESMA, delicate threads or fibrils of cytoplasm that pass through the walls of adjacent cells, establishing protoplasmic continuity.
- PLASTID, a specialized body occurring in the cytoplasm of a cell which may be colorless or pigmented. Cf. *Leucoplast, Chloroplast*.
- PLEROME, the layer or histogen from which the stele is derived.
- PLUMULE, the bud or growing point of the embryo.
- POD, a dry, many-seeded, dehiscent fruit; a legume, silique, etc.
- POLYARCH, (of root) a stele with several to many protoxylem groups.
- POME, a fleshy fruit developed from an epigynous flower in which the inner portions of the carpel wall are some-

- what thickened or, less commonly, membranous.
- ✓ **PROCAMBIAL STRAND**, the meristematic tissue that later develops as vascular tissue; more exactly, a provascular strand.
- PROCUMBENT**, lying along the ground.
- PROEMBRYO**, applied to the initial stages in embryogeny.
- ✓ **PROSENCHYMA**, a tissue in which the cells are elongated and tapered.
- PROTODERM**, the layer or histogen from which the epidermis is derived; dermatogen.
- PROTOPHLOEM**, the first elements of primary phloem to be differentiated.
- PROTOPLAST**, the cytoplasm and nucleus of a cell.
- ✓ **PROTOSTELE**, a solid stele with phloem surrounding a central core of xylem.
- ✓ **PROTOXYLEM**, the first elements of primary xylem to be differentiated, characterized by annular, spiral, or reticulate secondary walls.
- PUBESCENT**, covered with soft hairs.
- RACEME**, a simple indeterminate flower cluster with a central axis that is more or less elongated.
- RACHILLA**, a secondary axis in the inflorescence of grasses; the axis of a spikelet.
- RACHIS**, the axis of a spike.
- RADICLE**, the hypocotyl and rudimentary root of the embryo.
- RAPHE**, the ridge of an ovule extending from the hilum to the chalaza.
- ✓ **RAY**, (of flowers) the branch of an umbel; the marginal flowers in radiate composites; (of axes) radially oriented sheets of cells, i.e., medullary, xylem, and phloem rays.
- RECEPTACLE**, the portion of the axis from which the floral parts arise; the torus.
- RENIFORM**, kidney-shaped.
- RETICULATE**, in the form of a network.
- RHAPHE**, see *Raphe*.
- RHIZOME**, a subterranean stem from which shoots and adventitious roots may arise; a root-stalk.
- ROOT CAP**, the protective structure surrounding the terminal meristem of the root, consisting of cells derived from the calyptrogen; the calyptra.
- ✓ **ROOT-STALK**, see *Rhizome*.
- SAGITTATE**, arrow-shaped.
- SAMARA**, an indehiscent winged fruit; a key fruit.
- SCALARIFORM**, (of xylem elements) with ladder-like secondary wall thickenings.
- SCAPE**, a leafless floral axis arising from the ground.
- SCARIOUS**, thin, dry, and membranaceous, not green.
- SCHIZOCARP**, a fruit derived from a compound pistil in which the one-seeded carpels separate from one another at maturity.
- SCHIZOGENOUS**, applied to a cavity formed by the splitting of cell walls along the middle lamellae. Cf. *Lysigenous*.
- SCLERENCHYMA**, supporting or protective tissue in which the cells have hard, lignified walls and usually little protoplasmic contents at maturity.
- SCUTELLUM**, the cotyledon of an embryo of a grass.
- SEED**, (in angiosperms) an embryo or embryos with or without an external food reserve, surrounded by a covering which is generally integumentary.
- SEMINAL**, relating to the seed.
- SEPAL**, one of the members of the calyx.
- SEPTATE**, divided by partitions.
- SEPTICIDAL**, dehiscence of the ovary along the septa between the locules. Cf. *Loculicidal*.
- SERRATE**, with sharp teeth.
- SESSILE**, without a stalk.

- SHOOT, the stem and its appendages.
- ✓ SIEVE PLATE, the perforated area of a sieve tube.
- ✓ SIEVE TUBE, an element of the phloem with lateral or terminal sieve plates.
- SILIQUE, the dry, many-seeded, dehiscent (infrequently indehiscent) fruit of the Cruciferae, consisting of two carpels which form a bilocular ovary with a longitudinal septum.
- ✓ SIPHONOSTELE, a vascular cylinder surrounding a central pith.
- SPATHE, a large bract or bracts enclosing an inflorescence.
- SPATULATE, oblong with the basal end attenuated.
- ✓ SPIKE, a racemose inflorescence with sessile flowers on an elongated axis.
- SPIKELET, a secondary spike; the unit of the inflorescence in grasses.
- ✓ SPONGY TISSUE, parenchyma with many intercellular spaces.
- SPOROPHYLL, a spore-bearing leaf. Cf. *Mega-* and *Microsporophyll*.
- ✓ STAMEN, a pollen-bearing organ; a microsporophyll.
- STAMINODIUM, an abortive, sterile, or rudimentary stamen.
- STANDARD, the large upper petal of a papilionaceous corolla.
- STELE, the vascular cylinder of an axis; the central cylinder.
- ✓ STIGMA, the receptive portion of the pistil.
- STIPULE, an appendage at the base of the petiole.
- STOLON, a runner or prostrate stem that tends to root.
- STOMA (pl. STOMATA), an opening in the epidermis leading to an intercellular space.
- STOMIUM, an opening in an anther between lip-like cells through which dehiscence occurs.
- STONE CELL, an approximately isodiametric sclerenchymatous cell.
- STRICT, straight, upright.
- STYLE, the usually elongated portion of the pistil connecting the stigma and ovary.
- STYLOPODIUM, a disk-like enlargement at the base of the style.
- SUPERIOR, (of ovary) free from the other floral parts which are hypogynous.
- SUSPENSOR, (of embryo) the part of the proembryo at whose apex the embryo proper develops.
- SUTURE, a seam or line of union; frequently a line of dehiscence in fruits.
- SYMPETALOUS, see *Gamopetalous*.
- SYMPODIAL, (of stem) made up of a series of superposed branches so that it resembles a simple axis.
- SYNCARPOUS, of undiverged or "united" carpels.
- SYNERGID, the nuclei or cells adjacent to the megagamete at the micropylar end of the megagametophyte.
- ✓ TAPETUM, the layer or layers of cells adjacent to the sporogenous tissue in the micro- and megasporangium.
- TERETE, circular in transection; cylindrical and usually tapering.
- TESTA, the seed coat.
- TETRACYCLIC, (of flower) applied to one with four whorls of floral parts.
- TETRARCH, (of root) a stele with four protoxylem groups.
- TISSUE, a group of cells of common origin having essentially the same structure and performing the same functions.
- TORUS, the receptacle of a flower.
- TRACHEA, a xylem element consisting of ✓ a linear series of cells which form a continuous tube owing to the disintegration of their end walls; a vessel.
- TRACHEID, an elongated, water-conducting xylem cell with variously thickened and pitted walls.
- TRIARCH, (of root) a stele with three protoxylem groups.

- TUBER, a relatively short, thickened rhizome with numerous buds.
- TUNICA, the peripheral layer or layers of the apex of the shoot.
- TYLOSE, the intrusion of a protoplast into a vessel.
- UMBEL, a flower cluster in which the pedicels arise at about the same level on the peduncle.
- UMBELLLET, a secondary umbel.
- UNDULATE, with a wavy surface.
- VACUOLAR MEMBRANE, the limiting membrane separating the cytoplasm from an enclosed vacuole.
- VACUOLE, a cavity in the cytoplasm containing cell sap.
- VENTRAL, applied to the anterior or inner face of an organ.
- VERNATION, the arrangement of leaves in a bud.
- VERSATILE, (of anther) attached near the middle and turning freely on its support.
- VESSEL, see *Trachea*.
- VESSEL SEGMENT, one of the cells comprising a vessel.
- WHORL, an arrangement of leaves or floral parts in a circle around the stem.
- XYLEM, a complex vascular tissue which may include tracheids, vessels, fibers, parenchyma, and frequently ducts or glands.
- ZYgomorphic, (of flower) capable of division in only one plane of symmetry.
- ZYGOTE, the product of the union of two gametes; a fertilized egg.

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